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BIOLOGY OF CERTAIN CHIRONOMIDAE REARED FROM POTAMOGETON

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BIOLOGY OF CERTAIN CHIRONOMIDAE REARED FROM POTAMOGETON

INTRODUCTION

Chironomidae constitute an interesting and important part of the insect fauna directly related to plants of the genus Potamogeton in Michigan waters. In an earlier paper (Berg 1949) 32 species of insects, including 17 species of Diptera, intimately associated with these plants were listed, but none were discussed in detail. Areas studied, species of plants collected in each, and general habits and relationships of the insect fauna were recorded. An account of the biology and morphology of 8 acalyptrate Diptera is in press. Similar data concerning 9 species of Chironomidae will be presented here.

Acknowledgments are gratefully made to Professor Paul S. Welch, under whose guidance this work was carried out; to O. A. Johannsen, Cornell University, for original descriptions of 2 species and identification of one other; and to H. K. Townes, United States National Museum, for identifications of 4 species and original descriptions of 2 others.

The nomenclature of Townes (1945) is followed for all species within the scope of his monograph, with the exception that the well-known family name "Chironomidae" is retained in favor of the less familiar "Tendipedidae." Johannsen's nomenclature (1937, 1942, 1943) is followed for the subfamily Orthocladiinae.

Because of conflicting published statements, it seems advisable to review the literature before undertaking a discussion of the Chironomidae which feed upon Potamogeton. Frost (1924: 31-32) wrote: ". . . none of the Chironomidae are true leaf miners . . . because they do not work between the two epidermal layers of the leaves . . . *Cricotopus sylvestris* Fabr. and *Chironomus brasenae* Leathers, are the only known species of Chironomidae which feed on living plant tissue. The others all attach themselves to the leaves by means of silk, and feed on algae and diatoms which may come their way."

It seems that Frost overlooked the fact that Thienemann (1909: 146-8) and Gripekoven (1914: 135-6, 209-14) had described the habits of a true leaf miner, *Cricotopus brevipalpis,* and the possibility that subsequent investigations might reveal other leaf miners among undescribed Chironomidae or among described species, larvae of which were unknown. Several herbivorous species have been recorded in addition to the 2 listed as "the only known species . . . which feed on living plant tissue." Among those whose habits have been known for many years might be mentioned *Tanytarsus quadripunctatus* (Malloch) (Needham 1908, as *"Chironomus albistria* Walker"), *Chironomus nymphaeae* Willem (Willem 1908), *Cricotopus trifasciatus* (Panzer) (Willem 1910, as *"C. limnanthemi* Kieffer"), several species of Tendipes and Cricotopus discussed by Gripekoven (1914), and the species of *"Chironomus"* and *"Tanytarsus"* listed by Moore (1915). Finally, in stating that all other Chironomidae have the same habitat, mode of attachment and food, Frost has overlooked the free living, predaceous Tanypodinae; those larvae which burrow in living plants, Spongilla and Plumatella tissues, and bark (Gripekoven 1914: 133-5, 141-2); the littoral, sublittoral and profundal muck dwellers; those Diamesinae, Orthocladiinae and others which build cases on the rocks in intertidal zones and swift-flowing streams; the larvae which live within bodies of snails (Barnard 1911); the Symbiocladius and Spaniotoma larvae which live attached to Mayfly and stone-fly nymphs (Claassen 1922, Johannsen 1937); the terrestrial species which live in moss, rotten wood, potatoes, dung, and humus, some of which feed on root hairs and have become known as greenhouse pests; and others.

CLASSIFICATION ACCORDING TO FEEDING HABITS

It is convenient to classify the chironomid larvae which are intimately related to plants of the genus Potamogeton into 3 groups on the basis of their feeding habits. The accuracy of this system of classification is limited by the facts that some differences exist within each group and that a species which feeds in 2 ways combines the characteristics of 2 groups. Nevertheless this classification is useful in arranging the species which have basically similar feeding habits together. The literature on larvae of Chironomidae reared from hydrophytes other than Potamogeton indicates that this system of classification may have general applicability to plant-inhabiting species of this family.

Leaf Miners

Group 1 comprises the true leaf miners, which make linear mines between the 2 epidermal layers of the leaves. These larvae apparently do not spin silken tubes within their mines, which they extend almost continuously as they feed on mesophyll tissue. Two of the species included in this group were not known prior to this study, and other authors have not recognized this assemblage. Besides *Cricotopus brevipalpis* Kieffer, the biology of which was presented by Thienemann (1909) and Gripekoven (1914), it contains *C. elegans* Johannsen and *C. flavipes* Johannsen, the habits of which are reported here. Inasmuch as the excavations made by these larvae are the only ones which are comparable in

position, extent, and function with those of the terrestrial insect leaf miners, it seems appropriate to restrict the term "mine" to designate only this type of excavation.

FEEDERS ON SUPERFICIAL LEAF TISSUES

Group 2 embraces those larvae which feed on one epidermis and the mesophyll layer of leaves but leave the other epidermis intact. Insofar as these are larvae which live in open channels produced by their feeding activities, this assemblage equals Gripekoven's "Gruppe 2, oberflachlich Minierer," and Group IV of Leathers (1922). These larvae live in silken tubes, spun within the channels of all channeling species and laden with detritus. *Polypedilum ophioides* Townes, a leaf eater which does not produce nor occupy well defined channels, is included in this group because it subsists on tissues of upper epidermis and mesophyll. Channeling species included in this assemblage are *Cricotopus trifasciatus* (Panzer) and *Polypedilum illinoense* (Malloch), the larval habits of which are discussed here, and several species previously reported from Potamogeton and other hydrophytes, such as *Cricotopus sylvestris* (Fabr.) (Frost 1924), a few species of *Cricotopus* reported by Gripekoven (1914), and *Polypedilum braseniae* (Leathers) (Leathers 1922). Since the word "channel" clearly denotes superficiality of position, it seems preferable to such terms as "mine," "half-mine," and "burrow" to designate the usual type of excavation made by larvae in this group.

NET-SPINNING PLANKTON EATERS

Group 3 contains the net-spinning plankton eaters, most of which live in short burrows just beneath the epidermis of stems or leaves. These excavations, which rarely exceed twice the lengths of their occupants, are oriented longitudinally in the plant tissue, and they open at both ends, usually by means of roughly circular holes gnawed through the epidermis. A tube of closely woven silk lines each burrow throughout, and a conical silken net of relatively open weave is usually stretched across it just behind the larva.

Specimens of this group produce currents through the burrows by dorsoventral undulations of their bodies. Some investigators have ascribed only a respiratory function to these currents, maintaining that the chironomids subsist primarily on spermatophyte tissue. It has been demonstrated for at least 9 species, however, that the larva of each feeds on plankton filtered from the water as it passes through the conical net. Periodically, each larva turns about in the burrow, devours net and contents, weaves a new net, again reverses its position, and resumes rhythmic undulations of the body which produce a current through the burrow and into the net.

Not all specimens of this group live in stem burrows. Some silken tubes are spun in folds or rolled edges of leaves, and previous investigators have reported them on or within several types of substrata other than tissues of hydrophytes.

Larvae of most species in this group seem to consume very little spermatophyte tissue and to do so only incidentally when enlarging their burrows or excavating new ones. They apparently are related to Potamogeton for protection rather than for food.

This assemblage seems to be comparable with Gripekoven's "Gruppe 1," and with Leathers Group I. It includes *Glyptotendipes lobiferus* (Say), *Glyptotendipes dreisbachi* Townes, *Polypedilum sordens* (Wulp), and *Tanytarsus nigricans* (Johannsen), whose biologies are discussed here; *Microtendipes pedellus* (De Geer) and *Tanytarsus obediens* Johannsen, observed and reported by Leathers (1922); and *Glyptotendipes glaucus* (Mg.), *Glyptotendipes imbecillis* (Walk.), and *Polypedilum tritum* (Walk.), recorded by Burtt (1940).

Several additional species which probably belong to this group have been discussed by Willem (1908), Thienemann (1909), Goetghebuer (1913), Gripekoven (1914), and Wesenberg-Lund (1943). However, it will not be certain that these larvae exhibit all characteristics listed for Group 3 until their food habits have been investigated more thoroughly. Considerable information might be obtained by studying them and other chironomid larvae, including plant burrowers, burrowers in other substrata, and non-burrowing species, using the simple techniques employed here to observe feeding habits. The burrows made by these larvae are of the type described for Group 3. Like larvae of Group 3, larvae of these species also produce currents through their burrows by means of dorsoventral undulations of their bodies. Although plankton nets within the burrows were not known and the remarkable sequence of feeding activities was not understood, the descriptions of larval activities presented by Willem (1908: 698) and Gripekoven (1914: 137) would fit larvae of Group 3 very well. Willem actually stated that larvae living in such situations feed on plankton which is brought into their burrows by the currents which they produce.

Characterizations of this group by Gripekoven (1914: 140) as a "typischen Miniergruppe" and by Wesenberg-Lund (1943: 524) as "die typischen Blattminierer" evidently are incorrect. The habits of these larvae differ from those of typical insect leaf miners in 3 fundamental respects. Their excavations do not increase in length at a rate even approximating that of the typical leaf miners. They live in dead and decomposing portions as well as in living parts of the plants. Burrows of some species are often found in several types of substrata other than aquatic plants, and some attach their silken tubes superficially without making any excavation.

A mining larva which subsists principally on tissues of the plant which shelters it must either extend its excavation at approximately regular and frequent intervals as it feeds, or often abandon it and make new excavations. In Thienemann's illustration (1909: Fig. 19), reprinted by both Gripekoven (1914) and Wesenberg-Lund (1943), the sum of the lengths of 13 *Tanytarsus stratiotes* burrows is less than twice the sum of the lengths of the larvae occupying them. Yet not one empty burrow is shown. Evidently, bur-

rows which are extended only as their occupants grow and require more room, as seems to be the case in this group, function more as havens of refuge and seclusion than as typical food mines. It follows that larvae which occupy such burrows must have an important source of food other than the tissues of plants in which they live.

Leathers (1922: 9) reported on one of the species known to live in or on substrata other than tissues of living plants. He stated that, besides occurring in nearly all the submerged aquatics, the "burrows of *Chironomus* [*Glyptotendipes*] *lobiferus* may be found on floating logs, at the bottoms of ponds, or attached to stems, stumps, and other perpendicular surfaces." *Tendipes gripekoveni* Kieffer, which Townes (1945) considers identical with *G. lobiferus*, is recorded by Gripekoven (1914: 166-8) as occurring in aquatic plants of 4 genera including, "alten abgestorbenen Stücken von *Scirpus lacuster*," and, "in alten Eichenrinde . . . und . . . in Stöcken von *Plumatella fungosa*." While a plankton-eating species would appear capable of living in or on a variety of substrata, it is difficult to conceive of any true leaf miner altering its food habits so drastically as life in these different substances would seem to demand.

Considering the facts mentioned, it seems that no useful purpose can be served and much confusion and misunderstanding may result from continued reference to these species as "leaf miners." As an alternative, the term "burrower" is suggested. This term has the advantage of applicability to species which make or adopt short, protective excavations in any type of substratum, thus obviating the necessity of classifying any species in 2 or more groups simply because it lives in a variety of substrata.

Larvae of *Tanytarsus nigricans* (Johannsen) construct their silken tubes between rolled or folded leaves and seem to subsist partly on plankton and partly on leaf tissues. Since the plankton is obtained by producing a current through the silken tube in which a cone-shaped net filters out the particulate matter, and since the larva exhibits the typical sequence of feeding activities mentioned previously, this species is placed in Group 3, although it differs from most of the group in lacking the burrowing habit.

METHODS OF COLLECTION, REARING, AND OBSERVATION

FEEDERS ON LEAF TISSUES

Larvae of Groups 1 and 2 were brought into the laboratory in the leaves in which they were feeding, and kept in culture dishes about 220 mm. in diameter and 70 mm. high. Fresh leaves were supplied as needed, and aeration was maintained either by continuously bubbling air or by a continuous flow of aerated water through the culture dishes. The latter method, since it removed all dissolved and particulate wastes, and held the temperature at a constant, moderate level, kept the cultures fresher and was more successful. This method, however, required that a cylinder of copper screening be placed within the culture dish, emerging slightly above its rim, to keep the leaves from flowing out with the overflowing water. Larvae migrating from one leaf to another were frequently lost even when a screen cylinder of fairly fine mesh was used.

In order to observe larval activities, a single leaf was often removed from the culture dish and placed in a finger bowl or petri dish on the stage of a dissecting microscope. Larvae of Group 2, the leaf channelers, were studied almost entirely with reflected light. *Cricotopus flavipes* larvae, which mine in thin, transparent leaves, are more easily observed with transmitted light. Since larvae of *C. elegans* mine in thick, nearly opaque leaves, they are not clearly visible unless a piece of the epidermis covering them is removed.

Two methods were used to rear these Chironomidae. When positive association of larva, pupa, and adult stages was required, nearly mature pupae, with their last larval exuviae still adhering to their bodies, were carefully removed from their mines or channels and placed individually in test tubes. These tubes, each containing less than 10 cc. of water, were loosely stoppered with cotton and placed in a shallow tray in inclined positions providing maximum surface exposure to aerate the water. A stream of tap water which flowed continuously through the tray kept the temperature quite constant. In order to allow the skeleton of the imago to harden properly, a tube was not disturbed until at least 24 hours after emergence. At that time, the adult was usually resting on the cotton, and the larval and pupal exuviae were easily recovered from the water. These exuviae were dehydrated, mounted in balsam or clarite, and labelled. The adult was killed, pinned, and labelled with the same number.

It was found, however, that mass rearing resulted in less trouble and less mortality. This method was used whenever a collection was known to contain only 1 species, or when association of larva, pupa and adult stages of all species involved was already positively established. When pupation began to occur in a culture, a kitchen strainer was inverted over the dish, forming a canopy of fine mesh screening. A large size which fitted snugly around the rim of the culture dish worked especially well. A tube supplying aerated water was introduced through a small hole in the screen. Adult midges rested on the inside of this strainer and were collected by removing the water tube and introducing the tube of an aspirator in its place. Although these adults were kept alive until their skeletons were hardened, they were usually removed when first noticed and transferred to a dry container. Those left within the canopy frequently fell into the water and were drowned.

NET-SPINNING PLANKTON EATERS

Stem-burrowing larvae were brought into the laboratory in pieces of plant stems and kept in battery jars or small aquaria. These species are quite resistant to the toxic effects of decay products, and were easily maintained in the laboratory if aeration was supplied by bubbling air through the vessels.

When pupation began, battery jars containing these chironomids were placed in screen rearing cages, the aeration tube being introduced through a small hole in the screen. By providing 2 cages for each battery jar and shifting the jar from one to the other each morning, it was possible to make sure that no adult was killed until it was at least 24 hours old and the exoskeleton was well sclerotized. The first morning after emergence had begun, the jar was removed from cage 1 without disturbing the freshly emerged adults resting on the screen and placed in cage 2. The following morning, adults in cage 1 were killed and pinned, and the battery jar was shifted back into it without disturbing the adults in cage 2. When individual rearing was necessary, pupae were removed from their burrows and allowed to emerge separately in test tubes in the manner described.

Larvae of *Tanytarsus nigricans* were brought into the laboratory in plants, folded or curled leaves of which sheltered their silken tubes. Like other species of Group 3, they proved quite hardy and required no more attention than that an air bubbler be provided in their battery jar or aquarium. Individual and mass rearings were conducted in the same manner with this species as with other species of Group 3.

Certain special techniques were required in order to study the feeding activities of Group 3 larvae. Their positions in the plants naturally suggest that they subsist mainly on spermatophyte tissues. Stomach analysis, however, showed little or no Potamogeton tissue, the recognizable material being chiefly plankton. The question of how this plankton is obtained could not be answered without securing better visibility of the larvae than was possible in their natural burrows.

Modification of a technique suggested by Leathers (1922: 4; Fig. 26, p. 56) afforded excellent visibility of larval activities. Several capillary glass tubes, slightly larger than the mature larvae, were cemented side by side to a rectangular glass cover slip. A similar cover slip was then cemented to the exposed sides of these capillary tubes. This preparation was placed in a watch glass filled with water, together with several larvae which had been removed from their burrows. In a few hours most of the larvae had spun their silken tubes within the capillary glass tubes. They could then be studied with a microscope by both transmitted and reflected light, or the preparation containing them could be removed from the watch glass and placed in a miniature aquarium mounted in a lantern slide projector (Berg 1948), in order to demonstrate larval activities by projecting images of the larvae onto a screen.

The silk of which the cone-shaped nets are constructed is quite transparent and invisible in its natural condition even in these glass preparations. Leathers (1922: 5) reported that Ehrlich's acid hematoxylin stains this substance, but this stain cannot be used on living material. Addition of a suspension of powdered carmine or ultramarine blue to the water passing through the net gives it a coating of colored particles. Its existence, shape, position and the fact that larvae devour it and its contents then become evident. The carmine is only partially dissolved by digestive enzymes. Both carmine and ultramarine blue, which does not dissolve to any noticeable degree, are easily recognized even in small quantities in fecal pellets. Their passage through the transparent bodies of the larvae can be traced readily, and they give a reliable index of progress of particulate material through the digestive tract. The larvae suffered no apparent ill effects from ingesting these stains, but they did not eat nets which were too heavily loaded with either substance.

BIOLOGY AND MORPHOLOGY OF EACH SPECIES STUDIED

Cricotopus elegans Johannsen

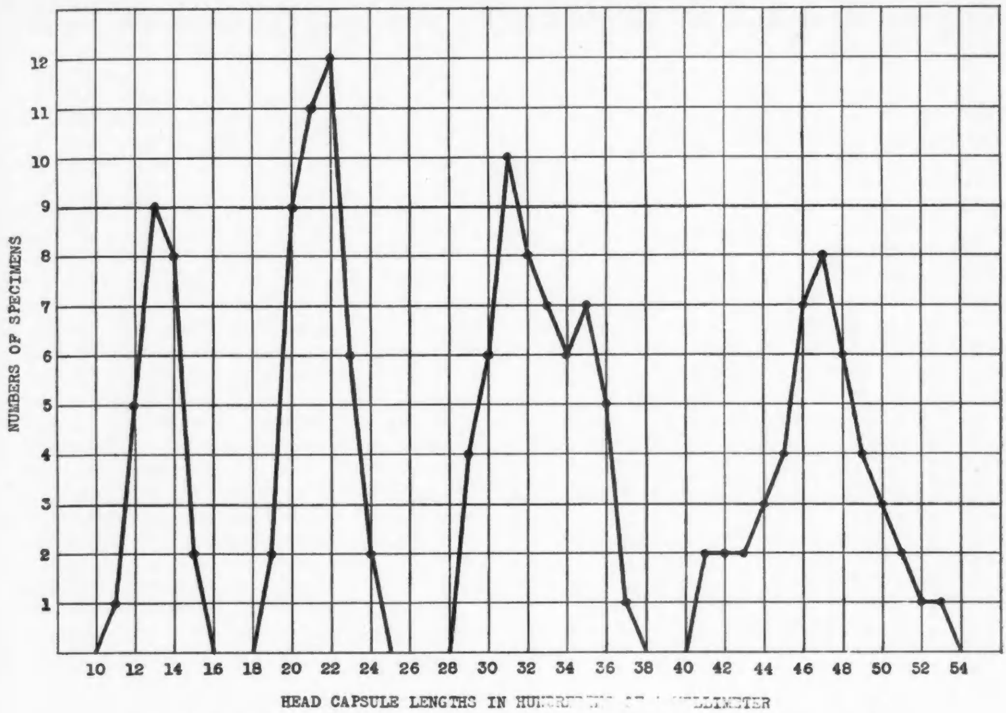
It appears that the only published reference to *Cricotopus elegans* is the original description of larva, pupa and adult stages (Johannsen 1943), which was based upon specimens collected and reared in this investigation.

C. elegans was encountered, May through October, in Livingston, Presque Isle, and Washtenaw Counties, Michigan. During most larval instars, specimens of this species mine in the coriaceous floating leaves of *Potamogeton amplifolius, P. natans,* and *P. nodosus.*

Measurement of the head capsules of 166 *C. elegans* larvae (Graph 1) showed that they belong to 4 distinct size groups composed of 25, 42, 54, and 45 individuals, respectively. The specimens measured were collected while they were in first or in second size group, then reared in culture dishes in the laboratory. After shedding head capsule exuviae of size group 1, larvae had heads of group 2. Changes from second to third and from third to fourth size group were also observed. Larvae with heads of group 4 invariably pupated at their next molt. It appears quite evident, therefore, that these 4 size groups correspond to the last 4 larval instars.

Eggs were not obtained and larval instars could not be positively identified by observation of hatching and all subsequent molts. Branch (1923) and Sadler (1935) have observed complete life cycles of *"Chironomus cristatus* Fabr." and *Tendipes tentans* (Fabr.) (as *"Chironomus tentans* Fabr."), respectively. They stated that each includes only 4 larval instars and that head capsule sizes for all specimens of a given instar are relatively uniform. For convenience in referring to instars of *C. elegans* represented by the 4 size groups, they may be numbered first, second, third, and fourth, if it is assumed that this species has the same number of larval instars as *"C. cristatus"* and *T. tentans.* The possibility that an unobserved instar may precede the one represented by size group 1 must be recognized, and the tentative nature of these instar numbers should be borne in mind.

According to Graph 1, mean lengths of larval head capsules along the median line from posterior rim to tip of extended labrum are 0.132 $\pm$0.0022, 0.214 $\pm$0.0010, 0.326 $\pm$0.0015, and 0.467 $\pm$0.0024 mm., for first, second, third, and fourth instar larvae respec-



GRAPH 1. Distribution of *Cricotopus elegans* larvae according to lengths of head capsules.

tively. Ranges in head lengths within the 4 groups are 0.05, 0.06, 0.09, and 0.13 mm.

Increments of growth between means of successive size groups are not a constant percentage of the smaller mean, as might be expected on the basis of Dyar's Law, but gradually decrease. The increment between means of size groups 1 and 2 is 62% of the mean of group 1; that between means of groups 2 and 3 is 52% of the mean of group 2; and the increment between means of size groups 3 and 4 is 43% of the mean of group 3.

Johannsen (1943) included no figures in his description of immature stages. Since all specimens sent to him were faded by preservation in alcohol, he does not mention color patterns characteristic of living material.

Mandible, antenna, and labial plate of the mature larva are shown in Figures 1-4. Since the latter normally is quite convex, it is impossible to see all of its teeth from any angle unless the plate is flattened as shown in Figure 4.

Coloring of the larva during late first, second, third, and early fourth instars is unusual and distinctive. The head is dark brown. Pro- and mesothorax are pale stramineous. Metathorax and first abdominal segment contrast sharply with these, being much darker with considerable violet color mixed with brown. Violet pigment gradually fades through the next 3 abdominal segments, which are predominantly brown. Posterior to these, olivaceous pigment arises and gradually increases, and in the last 3 segments this bluish olive color almost completely covers the brown.

Older fourth instar larvae, excluding their dark brown head capsules, and young pupae are pale stramineous throughout. Older pupae show more and more definite markings as color patterns of future adults develop within. Posterior end of the pupa is shown in Figure 5.

Each leaf infested by larvae of *C. elegans* usually harbors several specimens, the number of young larvae per leaf tending to be higher than that of older specimens. More than 20 first instar larvae often riddle a leaf with an irregular network of crisscrossing mines. It is uncommon, however, to find more than 3 third instar larvae in one leaf. Since all young larvae present in a group of several leaves floating close together usually are concentrated in only 1 or 2 of the leaves, it seems likely that eggs are deposited in masses on or near Potamogeton leaves, that newly hatched larvae tend to enter the nearest, most desirable, or most accessible leaf, and roam for short distances in search of fresh food as they grow older.

When leaves in which they are mining become brown and waterlogged, second instar larvae all abandon them within a few hours and start new mines in neighboring leaves. Their exuviae are left in the mines. Young third instar larvae often make another short migration, after which they immediately enter fresh leaves.

Later in the third larval stadium, many specimens

forsake their food leaves and swim about for a few hours, often settling on sides or bottom of the rearing dish, before reëntering the plant. Eventually, many of them start mining in submerged petioles, stems, and midribs. Fourth instar larvae in laboratory rearing dishes are usually found in these situations. Most specimens which remain in leaf blades throughout the third larval stadium leave this habitat early in the next stadium, swim about for some time, and enter one of these thicker portions of the plant. In the laboratory, 2 specimens remained in leaf blade mines during their entire larval lives and pupated there. The facts that last instar larvae were not found in the field and that older larvae in the laboratory abandon the plant and seem to hesitate for a few hours before reëntering it may indicate that they do not normally live on Potamogeton during this stage.

Pupation takes place in the mine, and the pupa remains there until it is mature and ready for the final molt, about 2.5 days later. Periodic vertical undulations of its body presumably cause some circulation of water in the mine and renew the supply of oxygen. When ready to leave the mine the pupa greatly increases the force of these movements and tears the plant epidermis. Then it swims up to the surface of the water, where the adult emerges. The pupal exuviae float freely on the water, but those of the last larval instar remain in the mines.

Since young larvae of *C. elegans* work within the leaf and leave both epidermal layers intact, they are true miners. Late in the third stadium, when larvae become greater in diameter than the thickness of leaves, those which continue to live in leaf blades begin to gnaw away the lower epidermis. From then on, they live not as true miners, but as channelers which are protected from above and at the sides by leaf tissue and from below by their detritus-laden silk tubes.

Cricotopus flavipes Johannsen

Larva, pupa and adult stages of *Cricotopus flavipes* were described and figured (Johannsen 1942) from specimens collected and reared in this investigation.

C. flavipes was encountered in Cheboygan, Presque Isle, and Washtenaw Counties, Michigan, in June, July, and August. The larva makes linear mines in the thin submerged leaves of *Potamogeton amplifolius, P. epihydrus, P. praelongus,* and *P. Richardsonii.*

Since all immature specimens sent to Johannsen were preserved in alcohol, he wrote nothing concerning natural colors of living material. Except for the light brown head capsule, larvae in the last 3 larval instars are entirely pale yellowish green. Pupae are of the same color when young, but show colors and markings of the future adult more and more distinctly as they grow older.

The larva of *C. flavipes* is strikingly modified for its particular mode of life. The leaves in which it mines are considerably thinner than the smallest diameter of the larva. In order to enter the very limited space between the layers of leaf epidermis and excavate the thin mesophyll layer, the anterior end of the larva's head must be much narrower than the rest of its body. The head capsule is wedge-shaped, its lateral compression becoming more and more pronounced toward the anterior end. Certain structures of the head have unusual shape, size, and orientation. The labial plate is so strongly convex ventrally that its most lateral teeth are invisible in ventral view unless it is forcibly flattened (Johannsen 1942: Figs. 3 & 4). The mandibles and premandibles are quite stout; the antennae, very minute.

Due to extreme compression of the head capsule anteriorly, bases of the mandibles almost touch each other. Thus it is impossible for tips of the mandibles to move in a nearly lateral plane, converging toward each other as they swing backward, in the manner which is almost general among larvae of nemocerous Diptera. Mandibles of *C. flavipes* move in a plane only a few degress from the vertical.

Assuming that the leaf is in normal position, the larva lies on its side when it mines. Regardless of leaf position, however, the larva is oriented with its sides in contact with the 2 epidermal layers. It extends both mandibles, one dorsal to the other, into the mesophyll tissue at the end of the mine and moves the head ventrally through an arc of about 120 degrees. At the end of this stroke the mandibles descend, one after the other, entering the narrow channel formed by the concave dorsal surface of the labial plate. The head then swings dorsally back to the starting position, where the mandibles are again extended and another working stroke is started. After making about 10 strokes in one direction, the larva backs for a distance of a few millimeters from the end of the mine, rolls over, crawls forward again, and makes a similar number of strokes in the opposite direction.

Mines of *C. flavipes* are readily distinguished from those of any Hydrellia species (Berg 1949) which might occur in the same leaves. Since this species removes all tissue between the epidermal layers, the mined area is left quite transparent and almost entirely without chlorophyll. This lack of color and the curved marks left by the mandibles, in groups which alternate regularly from side to side, are diagnostic when contrasted with the relatively uniform pale green color of Hydrellia mines. Mines of this species also differ in their tendency to be located near and parallel with the leaf margin.

All *C. flavipes* larvae found in leaf mines were in either last or next to the last larval instar, and there is good reason to believe that younger larvae have a different mode of life. On January 28, 1942, some larvae which appear to be *C. flavipes* in antepenultimate larval instar were found in longitudinal excavations in the stems of *P. Robbinsii* which was living beneath the ice in Whitmore Lake, Washtenaw County, Michigan. These larvae had the wedge-shaped heads, minute antennae, markedly convex labial plates, and other structures characteristic of *flavipes*. Since I was unable to rear them, the tentative identifications of these specimens is based upon their great similarity to larger larvae of *C. flavipes.*

Besides providing evidence concerning the mode of

hibernation of *C. flavipes* and the form and habitat of its younger larvae, the discovery mentioned supplies indications that these young larvae may utilize a type of food which is quite unusual among mining insects. Each mine that was opened contained quantities of algae which were identified by Wm. Randolph Taylor as Nostoc, Anabaena, Tolypothrix, Oscillatoria, Schizothrix, and Rhopalodia. These algae appeared to be alive and in good condition. Since each mine opened to the exterior by at least one hole through the epidermis, it is possible that the larvae brought small pieces of living filaments into the mines, and that the algae were growing as rapidly as they were being eaten. Unfortunately, no recognizable material was found in the stomachs of freshly killed larvae.

Measurement of head capsules of 70 *flavipes* larvae, including the small specimens mentioned, shows that they belong to 3 distinct size groups composed of 12, 17, and 41 individuals, respectively. The dimension used is the length along median line from posterior rim to tip of extended labrum. Heads in the smallest size group, all larvae collected in stems of *P. Robbinsii* in winter, were 0.22-0.24 mm.; average, 0.23 mm. Those in the next group, evidently the penultimate larval instar, were 0.33-0.38 mm.; average, 0.35 mm. Those of the largest size group, which is known to represent the last larval instar, were 0.50-0.60 mm.; average, 0.55 mm.

Transformations to last larval instar and to pupa occur in leaf mines, and exuviae of the last 2 larval instars are often recovered there. The pupa remains in the mine for a period of about 2.5 days, at the end of which it is mature and ready for the final molt. Then, by beating its body vigorously in a vertical plane, it breaks through the thin leaf epidermis and comes up to the surface of the water. Here the adult emerges, leaving the pupal exuviae floating on the water surface.

Cricotopus trifasciatus (Panzer)

Cricotopus trifasciatus was described (as *"Chironomus trifasciatus"*) in 1813. Immature stages were described by Johannsen (1905, 1937), Willem (1910, as *"Cricotopus limnanthemi"*), Goetghebuer (1914, as *"C. limnanthemi"*), Gripekoven (1914, as *"C. limnanthemi"* and *"C. Willemi"*) Malloch (1915), and Kettisch (1936-'37). Diagnostic characters of egg, larva and pupa stages are illustrated in these papers.

The biology of *C. trifasciatus* was first reported by Willem (1910), who found the larvae channeling in upper surfaces of floating leaves of *Limnanthemum nymphoides* at Gand in Belgium. Later, Gripekoven (1914) found the larvae feeding on leaves of *Potamogeton natans* and *Polygonum amphibium* at Eifel, Germany. Kettisch (1936-'37), who found the larvae feeding on the floating leaves of *P. natans* at Lunz, Austria, discussed the biology and metamorphosis in detail. Thienemann (1933) reported it from Eifel: Schalkenmehrener Maar, mining in *P. natans.* Johannsen (1937) stated that the species has a wide distribution in Europe and North America and that the larvae ". . . perhaps normally, mine in the leaves of the pond lily." It is evident from the foregoing account that *trifasciatus* feeds on the leaves of several species of aquatic plants.

In contradiction to these observations, Miller (1941: Table 14) has included this species with those "living below the thermocline." Although he did not find the larvae in his dredgings of profundal bottom materials, he captured 159 emerging adults in tent traps set over deep water and less than a dozen in similar traps set over shallow water among floating vegetation (personal correspondence). It is possible that the pupae migrate out to deep water when they leave the plants just before emergence.

C. trifasciatus was encountered in Cheboygan, Livingston, Presque Isle and Washtenaw Counties, Michigan. Larvae were found, May through August, channeling in the coriaceous floating leaves of *Potamogeton amplifolius, P. natans,* and *P. nodosus.*

Larvae enter the leaves from either the upper or the lower side, subsisting on one epidermal layer and the mesophyll tissue, but usually leaving the other epidermis intact. In a few instances in which the larvae had attacked leaves from their upper surfaces, the leaves were skeletonized so that only the veins remained. Once the leaf channel is formed, the larva is protected on 3 sides by leaf tissue, and on the other side by its detritus-laden silk tube, within which it is effectively concealed.

The larva frequently extends the anterior end of its body out of its silken tube and eats away the leaf tissue in irregular patches near the sides of its channel. When feeding outside its channel the larva gnaws approximately as deep as in extending its channel, usually leaving the further epidermis intact. In some instances, however, the portion of a leaf near an old channel is completely skeletonized.

Pupation occurs in the larval channel, and the pupa remains there until it is almost ready for the final molt. Dorsoventral undulations of its body periodically renew the supply of oxygenated water in the channel. From 1.5 to 3 days after pupation, these movements become more vigorous, and the pupa frees itself, leaving the last larval exuviae in the channel. It swims into open water, where the adult emerges, leaving the pupal exuviae floating freely on the surface.

Mating and oviposition of *C. trifasciatus* were described by Kettisch (1936-'37). According to her, specimens of this species pass the winter as eggs attached to stems and stipules of *P. natans.* I found as she reported that the speed of development of larvae and pupae tends to increase with rising temperatures.

Polypedilum (Polypedilum) illinoense (Malloch)

Polypedilum illinoense was described (as *Chironomus illinoensis,* Malloch 1915) from adults collected by sweeping vegetation along the bank of a creek at Carbondale, Illinois. Townes (1945) presented taxonomic, distributional, and seasonal notes, and placed it in the genus Polypedilum.

Apparently the immature stages of *P. illinoense* have not been described. The only published indica-

tion of their habitat seems to be that of Miller (1941: Table 14), who included them with "species living below the thermocline," on the basis of having collected emerging adults in tent traps set over deep water. Larvae of a closely related species, *P. braseniae* (Leathers) channel in the leaves of *Brasenia schreberi* and *Nymphaea odorata* (Leathers 1922).

Larvae of *P. illinoense* were encountered, May through October, in Cheboygan and Washtenaw Counties, Michigan, feeding on the floating leaves of *Potamogeton natans.*

The mature larva of *P. illinoense* is pale red or orange, about 5.5-6.5 mm. long. The larval antenna, labial plate, paralabial plate, and mandible are illustrated in Figures 19-21. Facts that the large blade on basal segment of antenna exceeds the apex of distal antennal segment, and that median pair of teeth on the labial plate are almost or quite as long as second lateral pair help to distinguish it from larvae of closely related species.

The pupa is faintly pigmented throughout. One of its most reliable distinguishing characters is the form of the comb on posterolateral angle of eighth abdominal segment (Fig. 22).

In habits and biology these larvae are very similar to those of *P. braseniae* (Leathers 1922) and *Cricotopus trifasciatus,* discussed above. All channel in floating leaves, feeding on one epidermis and the mesophyll tissue, either leaving the other epidermis intact or skeletonizing the leaf. This species often attacks the leaf on its lower surface. Sometimes they feed in their channels; often they gnaw away irregular patches of tissue adjacent to them.

Pupation occurs in silken tubes in the leaf channels, and the pupae remain there until several hours before their final molt. Then, by vigorous dorsoventral undulations of the body, they slip completely out of their last larval exuviae, out of their silk tubes, and into the open water, where they swim about near the surface for a few hours before the adult emerges.

Miller's (1941) recovery of teneral adults in tent traps set over deep water may indicate that pupae which develop in littoral weed beds of lakes normally swim out into the limnetic zone after leaving their leaf channels. It is difficult to conceive of any larva combining such totally unrelated habits as to live and feed sometimes on green, floating leaves and sometimes below the thermocline, as listed in Miller's Table 14, feeding on the limited materials available for food in the hypolimnion.

Polypedilum (Polypedilum) ophioides Townes

The description (Townes 1945) of *Polypedilum ophioides* is based in part on specimens reared during this investigation. Nothing has been published concerning its immature stages and biology.

In this study, mature larvae of *P. ophioides* were encountered in late June and early July in the Sedge Pools, Douglas Lake, Michigan, where they were feeding on floating leaves of *P. natans.*

The mature larva is pale red, about 5.5-6.0 mm. long. Its antenna, labial plate, paralabial plate, and mandible (Figs. 15-17) furnish valuable characters for recognition. Larvae of this species can be distinguished from those of the closely related *P. illinoense* by the shorter median pair of teeth on labial plate, the shorter large blade on basal segment of antenna, and by other characters illustrated.

The young pupa is very faintly colored throughout. Later the thorax and appendages are stramineous, abdomen pastel green, and compound eyes of the future adult appear as conspicuous black spots.

Position in relation to the leaf and feeding habits of this species differ from those of other larvae included in my Group 2, which live in well defined channels in leaves, extending them as they feed. Larvae of *P. ophioides* produce no distinct channels but feed by gnawing away the upper epidermis and mesophyll tissue in irregular patches. Some correlation may exist between the fact that these larvae lack the seclusion and protection afforded by such channels and the fact that they were found only in rolled lateral edges of young leaves, not exposed on flat leaf surfaces in the position of *P. illinoense* and *C. trifasciatus* larvae.

Pupation occurs in the leaf rolls, and exuviae of the last instar larva remain there. The mature pupa leaves this habitat about 2 days later, and swims out into open water, where emergence of the adult takes place.

Glyptotendipes (Phytotendipes) lobiferus (Say)

Glyptotendipes lobiferus, which was described as *"Chironomus lobiferus,"* is a relatively well known species, the immature stages of which have been described by Johannsen (1905: 233, 1937a: 37), Malloch (1915: 430), Leathers (1922: 7-17), and Branch (1931: 154). Of the several papers dealing with its biology, Gripekoven (1914, as *"Chironomus gripekoveni* Kieffer"), Leathers (1922), Fellton (1940), and Lindeman (1941, 1942) are especially informative. Townes (1945) elevated the subgenus Glyptotendipes to generic rank, cited literature dealing with this species, and presented notes on identification and distribution.

I found *G. lobiferus* in Third Sister Lake and Whitmore Lake, Washtenaw and Livingston Counties, Michigan. Some larvae were taken from burrows in stems of *P. amplifolius,* and *P. gramineus;* others were found in silken tubes in rolled or folded leaves of these species and of *P. Robbinsii.*

Some doubt may exist concerning the identity of my specimens. Fourth lateral labial teeth of these larvae are considerably smaller than those illustrated for *lobiferus* by Johannsen (1937a, Fig. 119). Johannsen (Fig. 118) shows 8 spines in the comb at posterolateral corner of eighth abdominal segment of pupa, but on my specimens these combs are composed of only 3-6 spines. According to Johannsen (1937a: 37), the mace-like processes at bases of pupal abdominal tergites 2-6 have lengths of 0.18, 0.21, 0.25, 0.29, and 0.53 mm., respectively. In 12 pupae collected in Third Sister Lake these relative lengths averaged 18: 20: 23: 27: 40. The mace-like process on abdominal segment 6, the width to length ratio of which averaged 9: 18, is considerably shorter than

the one illustrated by Johannsen (Fig. 131), in which this ratio is 9: 24. Although Townes wrote (personal correspondence) that my adult specimens "are atypical in being smaller and darker than usual and in having the scar on the sixth tergite much shorter than usual," he stated that these characters are subject to some variation and identified the specimens as *G. lobiferus*.

The remarkable feeding method employed by larvae of Group 3, that of capturing plankton in silken nets spun across the ends of their tubes, has been mentioned. The conical net is spun within and anchored to the silken lining of the burrow near one end, with its apex directed distally and its open end nearer the larva. The spinning motion consists of rapid extensions and retractions of the larva's anterior end as it slowly rotates, ostensibly to attach strands of the open end at points all around the circumference of the silk tube. After counting these extensions and retractions, Leathers (1922) concluded that the net is composed of 42-44 longitudinal ribbons or sheets. He discussed silk production and the mechanism of spinning in considerable detail.

The larva turns about after spinning its net, and makes rhythmic dorsoventral undulations of the body, like swimming movements of a leech, which progress backward from the head. Since the body is anchored by posterior prolegs to silken lining of the burrow and cannot move forward, these undulations force a current backward over the body and gills and into the open end of the net immediately behind.

After continuing these movements for a few minutes, the larva quickly reverses its position in the tube by bringing its head back along the ventral side of its body. Then it rotates the anterior end rapidly from side to side, cutting or tearing the delicate strands at the open end of the net near their attachment to heavier strands of the permanent silk tube. Continued rotation closes and twists up the net, and the larva, with thoracic prolegs aiding the mouth parts, stuffs net and contents into its mouth.

A short rest period often intervenes between eating the old net and spinning the new one, and the larva sometimes makes a vigorous current-producing motion of short duration during this interval. The purpose of this motion was unknown until I noticed that defecation occurs only during this time, and fecal pellets are forcibly ejected from the tube by this current. Since these pellets are thus carried some distance away from the tube, they are rarely brought in again by food currents, although these enter via the opening through which the pellets are expelled.

Defecation is similarly integrated into the sequence of feeding activities of all other species of this group herein discussed, and this is probaly true of all net-spinning plankton eaters. If defecation were indiscriminate, most of the fecal pellets would be caught in food nets.

Since these larvae normally defecate only during the relatively short period that their bodies are reversed from their usual positions in the tube, the statement of Willem (1908: 698) concerning *"Chironomus sparganii* Kieffer" seems highly questionable. He wrote, "Généralment, la larve est orientée la tête vers le haut, disposition que favorise l'evacuation des excréments par l'orifice inférieur." Although Leathers' suggestion (1922) that *"Chironomus sparganii"* is identical with *"C. lobiferus"* may be wrong, the former evidently belongs with *lobiferus* in Glyptotendipes (Phytotendipes) and probably feeds in the same manner. Willem's description and illustration of the pupa of *sparganii* include characters found only among species of Glyptotendipes (Phytotendipes), but he figures the labial plate of the larva as quite distinct from that of *G. lobiferus* larvae. His description of larval activities seems to be a discussion of net spinning, turning, current producing, and other movements of a net-spinning plankton eater written without knowledge of the food net and the sequence of feeding activities associated with it. If this is true, general orientation of larvae with heads upward indicates that feces are usually evacuated from the tubes via the upper openings, the fecal pellets being carried upward by the strong current produced by the larva during defecation.

To determine the approximate time spent in each of the major food-getting activities, 4 larvae were timed with a stop watch. Intervals spent spinning nets were 12-42 seconds; average of 13 records, 25 seconds. Intervals during which currents were produced through each net were 2-9 minutes; average of 12 intervals, 3 minutes 51 seconds. After reversing their positions in the tubes, the larvae loosened and swallowed the loaded nets in 7-40 seconds; average of 13 records, 19 seconds. One larva was slower than others in all 3 of these activities; another performed all 3 in the shortest time recorded for each. The times given by Leathers (1922) for these 3 activities are less than half a minute, 10 minutes, and 6 seconds, respectively.

The larvae found sheltered by Potamogeton tissues lived in silken tubes either in stem burrows or in young leaves which were still tightly rolled. Since water could circulate freely through each leaf roll, usually entering and leaving by means of 2 holes gnawed through all leaf layers approximately the same distance apart as holes opening into stem burrows, and since larvae removed from such leaf rolls spun their silken shelters within capillary glass tubes and there exhibited the characteristic sequence of feeding activities described, it seems probable that these larvae, like those living in stem burrows, subsist primarily on plankton and detritus strained from the water by their silken nets. When leaves once occupied by these larvae mature and unroll, they present a characteristic appearance, with 2 or more parallel, transverse rows of small holes, all holes of a row being approximately the same distance apart.

G. lobiferus larvae live in many different situations and feed by several methods. Leathers (1922: 9) stated that the larva "is capable of living in a loose mud burrow and of collecting and eating its food directly from the surface of the accumulated debris about it, but this is not its most characteristic method of feeding when living in competition with other species." Larvae observed in capillary glass tubes

augmented the food obtained from plankton nets by ingesting particulate matter collected both within and without their silken tubes. They frequently fed off inner surfaces of their silk tubes on materials which entered with currents they produced. Less often, a larva would extend the anterior end of its body to browse about and possibly forage on periphyton and other materials nearby.

Pupation occurs within the larval silk tube, and the pupa remains there until the adult is well formed within. Then it breaks out by vigorous dorsoventral undulations and swims about at the water surface for a short time preceding emergence. The observed pupal period was 1.5-2.5 days. The shorter records were obtained when air temperatures were relatively high.

As reported by Fellton (1940) reared and unmated females sometimes lay sterile eggs. Females which were reared and kept alone in test tubes sometimes deposited eggs during the night, about 72 hours after emergence. According to the descriptions of Branch (1931) and Fellton (1940), these masses were of normal shape, but none of the eggs hatched.

G. lobiferus larvae pass the winter in Potamogeton stem burrows and rolled leaves beneath the ice. When they are collected and brought into a warm laboratory they are quite active, and many feed by means of silken nets. The majority of specimens collected in January, February, March, and April were in last larval instar. These pupated and emerged 10-25 days after they were brought in.

Glyptotendipes (Glyptotendipes) dreisbachi Townes

Glyptotendipes dreisbachi was described by Townes (1945), who designated material reared in this investigation as part of the paratypic series. Apparently nothing further has been published concerning this species, and the immature stages have not been described.

Specimens of *G. dreisbachi* were encountered in Cheboygan, Livingston, and Washtenaw Counties, Michigan. Larvae were found throughout the year in burrows in the stems, petioles, and leaf midribs of *P. amplifolius*, *P. gramineus*, *P. praelongus*, *P. Richardsonii*, *P. Robbinsii*, and some aquatic plants of other genera.

The mature larva of *G. dreisbachi* is pale reddish orange, about 8-10 mm. long. Antenna, labial plate, paralabial plate, and mandible (Figs. 6-9) present characters of value in recognition. Although the convex labial plate appears in ventral view (Fig. 9) to have only 9 teeth, it actually has 13. A ventrolateral view (Fig. 7) shows 2 small teeth near the lateral border which are not visible in ventral view. This labial plate differs from that of most Glyptotendipes larvae in having the median tooth considerably smaller than the first laterals.

The pupa is about 6-8 mm. long. Its respiratory organs bear many white thread-like filaments. The second abdominal tergite has a row of small hooks along the posterior margin. Abdominal tergites 3-6 each have a median basal, spiked, mace-like process (Figs. 10-13) typical of *Glyptotendipes* pupae. The comb at posterolateral angle of eighth abdominal segment (Fig. 14) contrasts with those of most species in the genus in being reduced to 2 (sometimes 3) spines.

Although specimens of *G. dreisbachi* were encountered more commonly than those of any other chironomid species herein discussed and many adults were reared, attemps to get mating in the laboratory were unsuccessful just as they were with other species of Chironomidae. Since fertile eggs were not obtained and the complete life cycle was not observed, my information concerning larval instars is based only upon existence of distinct size groups of larval head capsules and upon observed transitions of larvae from one group to another. Measurement of 117 head capsules shows that they belong to 3 distinct size groups composed of 21, 37, and 59 specimens, respectively. Median lengths of these head capsules from posterior rim to tip of extended labrum are 0.20-0.24 mm., average 0.22 mm.; 0.31-0.40 mm., average 0.35 mm.; and 0.52-0.62 mm., average 0.58 mm. Since observed molts of smaller larvae always resulted in acquisition by the larva of a head capsule in the next larger size group and observed molts of the largest larvae always resulted in pupation, it seems quite evident that these 3 size groups correspond to the last 3 larval instars.

Larvae of *G. dreisbachi*, in all 3 instars encountered, exhibit the complex sequence of feeding activities characteristic of the net-spinning, plankton-eating species which are here placed in Group 3. It seems that these feeding habits are widespread among larvae of this genus. Those of 3 other Glyptotendipes species also are known to capture their food in silken nets (Leathers 1922, Burtt 1940), and those of still others (Willem 1908, Gripekoven 1914, Goetghebuer 1919) live in similar burrows and probably feed in this manner.

Several larvae were timed with a stop watch to determine lengths of time spent spinning food nets, producing currents through them, and eating them. Nets were spun in 20-58 seconds; average of 28 records, 36 seconds. Intervals spent producing a current through each net ranged from one minute 48 seconds to 8 minutes 20 seconds; average of 23 observations, 3 minutes 8 seconds. Animal plankters temporarily trapped in a food net though not entangled in its strands were sometimes observed to escape, but the larva's speed in turning about in the burrow and consuming the loaded net reduces loss of this type to a minimum. Nets were eaten in 8-45 seconds; average of 26 records, 20 seconds.

Many interruptions occur in the sequence of feeding activities associated with use of plankton nets. When a large particle enters the burrow, the larva usually ceases its rhythmic undulations at once, then makes several vigorous and rapid beats in a posterior-to-anterior direction, producing a strong counter current which generally ejects the particle. Since the conical net immediately collapses and closes, relatively little of its contents is swept out by these currents. If the particle is not thus expelled, the chi-

ronomid crawls forward and nips viciously at it. This action usually proves quickly effective against intruding larvae and other living animals, but fecal pellets may still adhere to the silken lining of the tube. When the larva cannot dislodge such materials with its mandibles and eject them either by vigorous counter currents or by carrying them to the entrance in its mandible, it leaves these substances in the burrow but isolates them from the open tube by spinning a patch of silken lining over them.

Counter currents are also produced by larvae which turn about to eat their food nets but find them very heavily loaded with carmine or ultramarine blue. A larva which has torn such a net loose and stuffed about half of it into the mouth often ejects it a considerable distance from the burrow by releasing it while producing a strong posterior-to-anterior current.

Other alterations of the normal pattern of feeding activities have no apparent causes. After producing a current through the net one chironomid turned about in the burrow, immediately spun a new net, then broke through it, ate the old net and its contents, spun another net, and resumed the normal sequence of activities. On another occasion a larva turned about, spun a new net within the old one, then turned back and produced a current through both nets. This larva left the outer net the next 2 times it turned about to eat and replace the inner one, but ate both nets the third time it turned toward them.

A larva sometimes eats the net, neglects to spin a new one, then turns about and produces a current through the burrow. When the larva turns back again it usually eats a bit of debris which adheres to the silk tube approximately where the net would normally be, and, again neglecting to spin a net, often turns and repeatedly produces currents through the burrow with no special provision for straining out the plankton. While some debris adheres to the silk tube, this is far less efficient than a plankton net for retaining food particles. After turning about a few times without spinning any net a larva often spins one in the end of the tube opposite from that in which nets had been placed before. Subsequent activities of the larva are all reversed in direction from previous ones, and food currents enter and excrement is ejected through the opening opposite that previously used.

By introducing suspensions of materials having different colors, the particles of which were caught in food nets and eaten, information on the speed of progress of particulate material through the alimentary tract was obtained. Two drops of a carmine suspension were released near the glass capillary tube in which a larva was producing a current through the net. The larva ate the net which was coated with these particles, and the next 2 nets which were left uncolored. The fourth net was given a coating of ultramarine blue, after which 2 more nets were left uncolored before carmine was released to color the seventh. As long as 2 nets were left uncolored between each release of stain, undissolved particles of stains mixed together very little in the intestine and most fecal pellets contained only one color.

Five larvae of *G. dreisbachi* living in glass tubes so close together that all were visible in the field of a dissecting microscope were fed alternately on carmine and ultramarine blue and watched for 3.5 hours. Undissolved particles of these stains passed through the alimentary tracts of 4 larvae in 35-124 minutes; average of 34 records, 69 minutes. Although the fifth larva seemed to go through the motions of spinning several times, most particles of stain passed completely through the tube, and it was evident that this larva spun no net during the period of observation. Since this specimen fed at frequent intervals on particles of debris and stain adhering to the silk tube, it was practically impossible to keep account of when certain particles were eaten and to recognize them again in fecal pellets. During these observations I noticed that these larvae defecate, as those of *G. lobiferus,* only after eating the old net, before spinning the new one. They defecated at intervals of 7-19 minutes; average of 23 records, 12 minutes.

Marked differences in the activities of these larvae were apparent. One consistently ate nets and spun new ones faster and nearly always produced swifter currents for shorter period of time than the average of the other 3. Two of the 4 larvae which spun nets continued to place them in the same ends of their tubes throughout the period of observation. One larva changed the position of the net and reversed the direction of its activities once; the other, twice.

A few larvae were observed through a dissecting microscope while enlarging their stem burrows. A specimen which had extended one end of its burrow about 5 mm. beyond the opening was evidently trying to make a new hole there. The mouthparts were clearly visible through the thin but yet unbroken epidermis. Labrum and mandibles all worked against the labium, which was moved relatively little. When observations were resumed after a short interruption a new opening was discovered where the mouthparts had been seen at work, and the old hole was sealed shut with silk. Suspended carmine flowed rapidly into the new opening and collected in a conical shape behind the larva. When the chironomid turned about it apparently found the net too heavily loaded with stain. It attempted to tear the net loose and to force it from the burrow by vigorous posterior-to-anterior undulations. Finally giving up these attempts, the larva moved its head to and fro across the net, apparently spinning at patch of silk over it, and left it there.

Larvae removed from their burrows and placed in a watch glass with some freshly cut pieces of stem excavated new burrows in 8-24 hours. These larvae always entered the stem via some cut edge, then made 1 or 2 holes through the epidermis from the inside.

Some larvae were killed soon after making new burrows, and their stomach contents were analysed by means of the sulphuric acid-iodine test for cellulose, to determine whether they had ingested Potamogeton tissue. Stomach contents were mixed with 1 or 2 drops of concentrated sulphuric acid on a glass

microscope slide, and a drop of potassium iodide solution saturated with iodine was stirred into the mixture. The dark blue color indicating the presence of cellulose appeared, and microscopic examination revealed that this color was produced in regular rows of rectangles which were easily recognized as fragments of spermatophyte tissue in which the natural pattern of cell walls remained intact. Stomach contents of larvae selected at random from old burrows showed little if any spermatophyte tissue when subjected to the same test.

Specimens of *G. dreisbachi* pass the winter as larvae, practically all of which are mature, in burrows in the stems of plants living beneath the ice. Apparently they remain more or less active throughout this season. All winter specimens which were observed, even those noticed before the collection had warmed up to laboratory temperature, were quite active. Specimens collected in winter and kept in aquaria at laboratory temperature pupated and usually began to emerge 11 days after they were collected.

My earliest record of pupae in nature is based upon 3 specimens included with many larvae collected at Third Sister Lake, Washtenaw County, on April 30, 1941. Emergence usually occurs in southern Michigan between May 15 and May 25, and most burrows in plants collected in late May and early June are empty.

Small larvae were taken in burrows in stems, petioles and leaf midribs of *P. praelongus* growing in Indian River, Cheboygan County on June 29, 1941. Since head capsules of the 11 specimens which were immediately killed and measured all belonged to the smallest size group (0.20-0.24 mm.) mentioned, it seems that most or all specimens in this collection were in an early larval instar. These larvae grew slowly in laboratory aquaria. Although 5 specimens examined on July 10 had head capsules in the intermediate size group, 5 others still had heads in the smallest group. Ten more larvae were killed and measured on July 17, and their heads also were divided evenly between these 2 size groups. All heads from specimens killed in the laboratory on August 7 and from others collected at Indian River on August 9 were in the intermediate group (0.31-0.40 mm.). None had molted and attained the last larval instar when they were examined again on August 21.

Larvae collected in Washtenaw County in September and October had head capsules in the intermediate and the largest size groups. A specimen in penultimate larval instar was taken in Third Sister Lake on November 3, but nearly all specimens found that late in the season were in last larval instar. It would seem from the facts mentioned above that *G. dreisbachi* has only one brood per season in Michigan.

The pupal period lasts 2-4 days, and the pupae remain within larval stem burrows during most of this time. Emergence occurs during the night. Mature pupae which had left their stem burrows were often seen swimming at the surface of the water, but such observations were invariably made at night.

Polypedilum (Pentapedilum) sordens (Wulp)

Polypedilum sordens was described (as *Tanytarsus sordens*) from the Netherlands in 1873. It seems that very little has been published concerning its biology, and that the immature stages are unknown. Townes (1945: 61-62) placed the species in Polypedilum, cited literature dealing with it, and presented notes on its identification and distribution.

I found *P. sordens* in Third Sister Lake, Washtenaw County, and Whitmore Lake, Washtenaw and Livingston Counties, Michigan. Larvae were collected from burrows in stems of *P. amplifolius, P. gramineus, P. natans, P. Richardsonii,* and *P. Robbinsii.* A few were taken in rolled or folded leaves of all these plants except *P. natans.* Burtt (1940) reported that a closely related species, *Polypedilum (Pentapedilum) tritum* (Walker), is also a stem-burrower which feeds on plankton strained from the water by means of a silken net spun within the burrow.

Larvae and pupae of *P. sordens* are easily distinguished, even with low magnification, from those of the 2 Glyptotendipes species I found in similar stem burrows. Mature larvae of all 3 species are pale red-orange, those of *P. sordens* about 6.5-8.5 mm. long, while larvae of Glyptotendipes are larger. The head capsule of *P. sordens* is depressed and bears only one group of ocelli on each side. Heads of the Glyptotendipes species are globoid and have 2 distinctly separate ocelli groups on each side. Pupae of *P. sordens* are 5-6 mm. long. They lack the conspicuous macelike processes found on abdominal tergites of Glyptotendipes pupae.

Characters which will help to distinguish *P. sordens* larvae and pupae from those of closely related species are illustrated in Figures 23-26. Larval antenna (Fig. 25) has the ring organ near base of first segment. Labial plate (Fig. 24) bears 16 teeth of fairly uniform length, with median pair somewhat heavier than others; paralabial plates are strikingly long and narrow. Comb at posterolateral angle of eighth abdominal segment of pupa (Fig. 26) is composed of 4 heavy spines and many smaller ones.

Since I was not able to observe the whole life cycle of *P. sordens,* my information on larval instars is incomplete. Measurement of 81 larval head capsules shows that they belong to 3 distinct size groups composed of 13, 21, and 48 individuals, respectively. The dimension used is median length from posterior rim to tip of extended labrum. After shedding head capsule exuviae of the smallest size group, larvae had heads belonging to the intermediate one. Changes from intermediate to largest size and from largest larva to pupa were also observed. Evidently these 3 size groups correspond with the last 3 larval instars. Probably an unobserved instar precedes that represented by the smallest recorded size group. Heads in these 3 size groups are 0.18-0.20 mm., average 0.19 mm.; 0.31-0.36 mm., average 0.33 mm.; and 0.46-0.62 mm., average 0.54 mm.

Like other larvae of Group 3, those of *P. sordens* subsist partly on plankton and detritus strained from

the water by their silken nets and partly on materials gathered outside or inside their tubes without using any net. Stomach analysis of specimens taken from burrows usually shows a preponderance of plankton organisms; larvae living in tubes on leaves often contain more periphyton than plankton. The stomach of one collected on a leaf of *P. Robbinsii* at Whitmore Lake, February 22, 1942, contained at least 25 diatoms, a piece of filamentous alga, and 4 small fragments of spermatophyte tissue.

Various operations in the sequence of feeding activities were timed with a stop watch. Food nets were spun in 17-50 seconds; average of 16 observations, 33 seconds. The interval during which a current was produced through the net was one minute 20 seconds-4 minutes 3 seconds; average of 17 records, 2 minutes 24 seconds. After turning about in their tubes, larvae ate nets and their contents in 8-18 seconds; average of 13 observations, 13 seconds.

Speed of passage of particulate material through the alimentary tract was determined in the manner described for *G. dreisbachi,* by alternately introducing different colored stains which were caught in food nets and eaten. Each stain-loaded net produced a colored mass, the progress of which could be watched through the partly transparent body of the larva. Since all particles of a given mass were eaten simultaneously and since these masses retained their identity with very little mixing of different colored particles within the intestine, the interval that each particle was retained could be determined quite accurately.

Particulate material passed through the alimentary tracts of 3 larvae in 33-77 minutes; average of 26 records, 57 minutes. It may be significant that the shortest intervals were always the first ones, when the intestines were relatively empty. As each alimentary tract filled on account of bulk of the stains, speed of passage through it gradually decreased. Apparently these stains did not harm the chironomids seriously and permanently; all 3 specimens later pupated and emerged. During these observations, I noticed that the larvae defecated at intervals of 9-16 minutes; average of 18 records, about 11 minutes, or approximately every third time they turned and ate their nets.

It may be that larvae of *P. sordens,* particularly those of earlier instars, are less able than those of *G. lobiferus* and *G. dreisbachi* to penetrate tough epidermis of living plant stems. Burrowing larvae of the 2 smaller size groups mentioned were almost always found in dead, partly decomposed stems, which they may have entered either by gnawing through softened epidermis, by penetrating the stem through breaks in the epidermis, or by occupying burrows vacated by Glyptotendipes larvae.

Specimens removed from their burrows and left in a finger bowl with freshly cut pieces of living *P. amplifolius* stem entered the stem in several instances, but invariably did so through a cut end, then penetrated the epidermis from within. Once inside the stem it would seem that they could exert more pressure on the epidermis because they can push back against parenchyma as they drive the mouthparts forward. Leathers stated that *G. lobiferus* enter Typha stems only through cuts or breaks, and can penetrate the very tough epidermis of that plant only from within. However, burrows of both *G. lobiferus* and *G. dreisbachi,* opening through the epidermis at both ends, are commonly found in living Potamogeton stems. Evidently these larvae penetrate the living epidermis of Potamogeton from either side.

Like other Chironomidae herein discussed, *P. sordens* pupate within larval silk tubes and remain there until mature, then swim about near the water surface for a few hours preceding emergence. In those instances in which both pupation and emergence were witnessed, the pupal stage lasted 1.5-2.5 days.

Unmated females laid masses of sterile eggs about 3 days after emergence.

Larvae of *P. sordens* pass the winter on or within tissues of Potamogeton beneath the ice. Specimens representing the last 3 instars occur in January and February collections, but fewer larvae of the smaller instars are collected toward spring.

My record of a reared specimen which emerged on May 3 (Townes, 1945: 62) bears little or no relationship to the natural seasonal aspects of this species. Specimens collected in late winter or early spring as last instar larvae and kept in a warm laboratory pupated and emerged 8-24 days later. Although I have reared adults in March and April as well as early May, they usually do not appear in nature in Washtenaw County until late May or early June.

Tanytarsus (Endochironomus) nigricans (Johannsen)

Tanytarsus nigricans was described (as *"Chironomus nigricans"*) by Johannsen (1905: 219), who included descriptions and illustrations of the larval and pupal stages. Immature stages have also been described by Malloch (1915: 434) and Johannsen (1937a: 34). Notes on its biology were presented by Richardson (1921: 42, 1925: 381, 418), Bill (1932: 68), Townes (1938: 172), Miller (1941: 35, 45, 61, 63), and Lindeman (1942: 435-6). Townes (1945: 64-5) placed the species in Tanytarsus, cited literature concerning it, and presented notes on its identification and distribution.

I collected *T. nigricans* in Huron River and Third Sister Lake, Washtenaw County, and in Black River, Cheboygan County, Michigan. Larvae and pupae were found in folds or in rolled edges of floating and submerged leaves of *P. amplifolius, P. gramineus, P. illinoensis,* and *P. Richardsonii.*

To some extent at least, the larvae obtain food by use of a net as described for larvae of Group 3. On one occasion, all 18 larvae in a rearing dish were feeding in this manner. Like larvae of *G. lobiferus* that live in rolled edges of leaves, *T. nigricans* larvae usually gnaw holes through all leaf layers at the ends of their silk tubes. These holes allow free circulation of water through the tubes, and the larvae may obtain some nourishment by swallowing the leaf tissue which they remove. Leaves once occupied by these larvae have a characteristic appearance when

they mature and unroll, bearing many small holes geometrically arranged in transverse rows. Most of the leaf injury of this type probably is caused by *T. nigricans*. Larvae on flat unrolled leaves often live within a roll of leaf epidermis which they presumably peel from the mesophyll layer beneath it.

Habits of these larvae differ in some ways from those of other species in Group 3. They seldom if ever occupy stem burrows. They obtain much of their food, including substantial quantities of Potamogeton leaf tissue, by foraging outside their tubes. Even while using food nets, *T. nigricans* larvae apparently eat some material besides that caught in the nets. They move the mouth parts almost continuously while producing currents through their tubes and seem to catch and devour a portion of their food directly.

Near the silken tubes of *T. nigricans* larvae, patches of leaf area which are white, devoid of chlorophyll, and sometimes completely skeletonized result from consumption of leaf tissue in these areas by the larvae. Application of the sulphuric acid-iodine test for cellulose (mentioned previously) to stomach contents and fecal pellets of larvae almost always resulted in production of the positive dark blue color. This color was often so well localized that it constituted a differentiating stain, and thus showed portions of undigested cell walls which were still arranged in normal patterns and were clearly recognizable as spermatophyte leaf tissues.

This method of feeding is very similar to that usually employed by larvae of *Polypedilum (Polypedilum) ophioides*, of Group 2. Larvae of *T. nigricans* seem to combine the feeding habits of Group 2 and Group 3 and may represent an incipient stage in the evolution of the remarkable feeding method employed by larvae of the latter group.

Pupation occurs within the larval silk tube, and the pupa stays there until almost ready for the final molt. Then it leaves this refuge and swims about near the water surface for a short time preceding emergence.

Lindeman (1942: 436) suggested that *T. nigricans* overwinters in the egg stage in Cedar Bog Lake, Minnesota. There is reason to believe, however, that larvae of this species pass the winter beneath the ice in Third Sister Lake. Larvae in last instar were abundant there during September, October, and November, 1941, and other mature larvae were collected there on March 30, 1942, about 2 weeks after ice on the lake had melted.

Emergence occurred at Third Sister Lake on May 3, 1942. On that date adult *T. nigricans* were flying near the lake shore, and others emerged in a pail of *P. amplifolius* while enroute from the lake to the laboratory. Adults may be reared in the laboratory during seasons when no emergence occurs in nature. Many were reared in connection with unsuccessful attempts to get mating in the laboratory during December, 1941.

SUMMARY

1. Biological data on 9 species of Chironomidae reared from plants of the genus Potamogeton in Michigan are presented.

2. The larvae are classified into 3 groups on the basis of their feeding habits.

3. Methods of collecting, culturing, and observing the larvae are explained.

4. Feeding methods of larvae, modes of hibernation and other seasonal aspects, larval instars, location and activities of pupae, and emergence are discussed in some detail.

5. Group 1, the leaf miners, includes *Cricotopus elegans* Johannsen and *C. flavipes* Johannsen, both of which were described from specimens reared in this investigation. These larvae make linear mines between the 2 epidermal layers of the leaves, extending them almost continuously as they feed on mesophyll tissue.

6. Group 2 comprises leaf channelers and other larvae which feed on one epidermis and the mesophyll layer of leaves but usually leave the other epidermis intact. It is represented by *Cricotopus trifasciatus* (Panzer), *Polypedilum (Polypedilum) illinoense* (Malloch), and *P. (P.) ophioides* Townes.

7. Group 3, the net-spinning plankton eaters, contains *Glyptotendipes (Phytotendipes) lobiferus* (Say), *G. (Glyptotendipes) dreisbachi* Townes, and *Polypedilum (Pentapedilum) sordens* (Wulp), all of which live in short burrows in stems and petioles, and *Tanytarsus (Endochironomus) nigricans* (Johannsen), which spins its silken tubes within rolled or folded leaves.

8. Larvae of Group 3 feed on plankton filtered from the water as it passes through conical silken nets spun across the tubes lining their burrows. Periodically, each larva devours net and contents, spins a new net, and resumes rhythmic undulations of the body which produce a current through the net.

9. Duration of various phases in the sequence of feeding activities of Group 3 larvae and speed of passage of particulate matter through the alimentary tract are recorded. Defecation apparently occurs only between certain phases in the cycle of feeding activities.

10. Immature stages of 5 species are figured and described for the first time.

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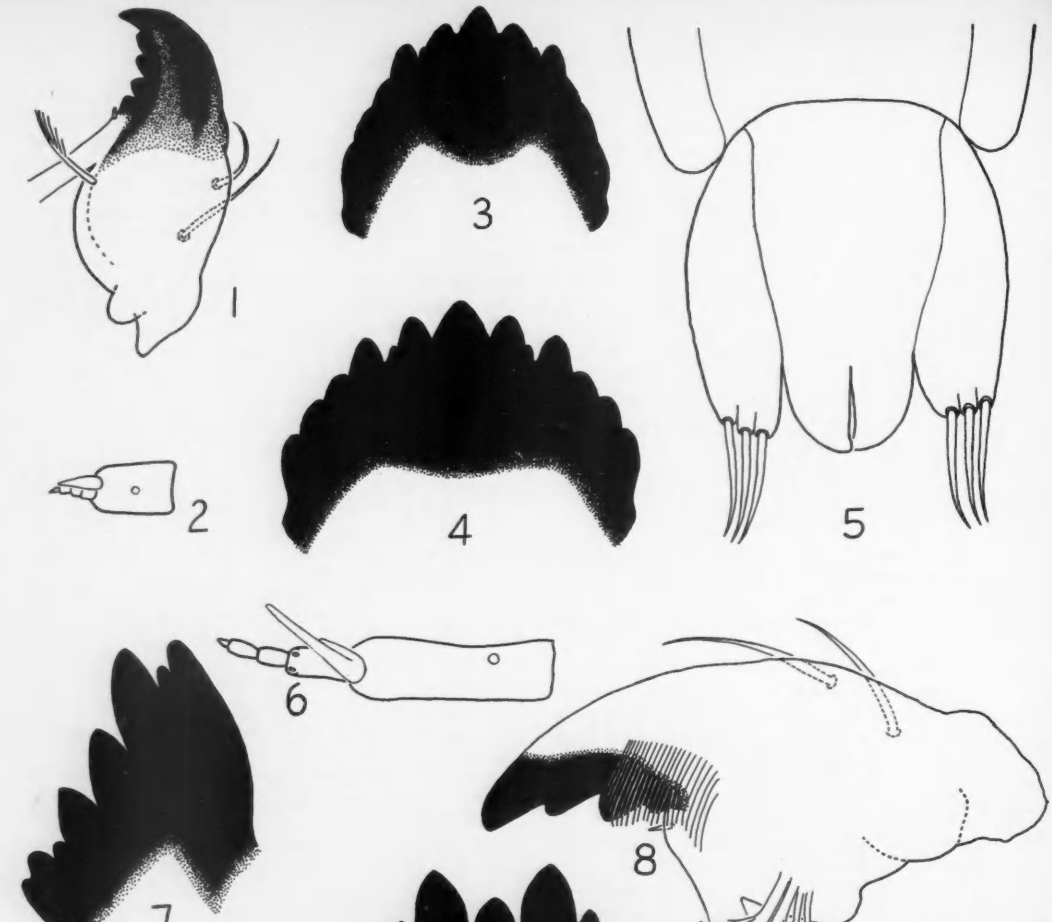

PLATE 1. Distinguishing characters of *Cricotopus elegans* and *Glyptotendipes dreisbachi* larvae and pupae

Fig. 1. *Cricotopus elegans:* Right mandible of larva in dorsal view.
Fig. 2. *C. elegans:* Antenna of larva.
Fig. 3. *C. elegans:* Labial plate of larva in normal convex shape.
Fig. 4. *C. elegans:* Labial plate of larva, flattened.
Fig. 5. *C. elegans:* Ninth and part of eighth abdominal segments of pupa.
Fig. 6. *Glyptotendipes dreisbachi:* Antenna of larva.
Fig. 7. *G. dreisbachi:* Labial plate of larva in right ventrolateral view.
Fig. 8. *G. dreisbachi:* Right mandible of larva in dorsal view.
Fig. 9. *G. dreisbachi:* Labial plate and right paralabial plate of larva in ventral view.
Figs. 10-13. *G. dreisbachi:* Mace-like processes on abdominal segments 3-6 of pupa, respectively.
Fig. 14. *G. dreisbachi:* Comb at right posterolateral angle of eighth abdominal segment of pupa.

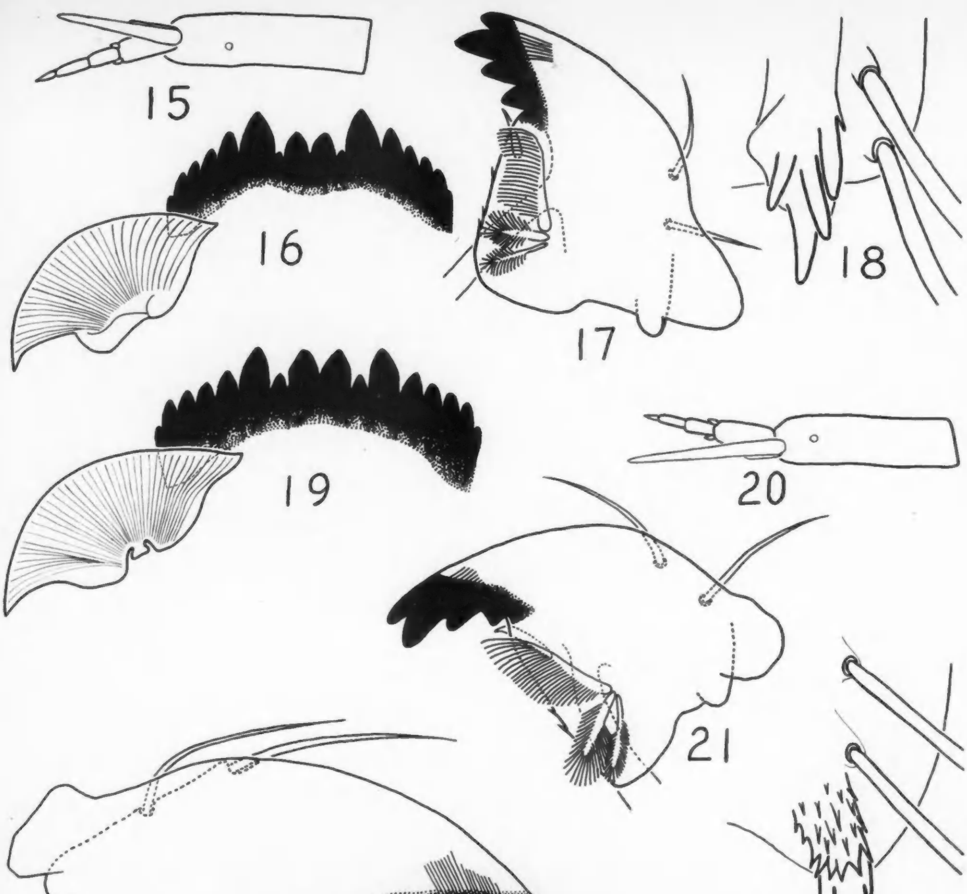

PLATE 2. Distinguishing characters of Polypedilum larvae and pupae

Fig. 15. *Polypedilum ophioides:* Antenna of larva.
Fig. 16. *P. ophioides:* Labial plate and right paralabial plate of larva in ventral view.
Fig. 17. *P. ophioides:* Right mandible of larva in dorsal view.
Fig. 18. *P. ophioides:* Comb at right posterolateral angle of eighth abdominal segment of pupa.
Fig. 19. *Polypedilum illinoense:* Labial plate and right paralabial plate of larva in ventral view.
Fig. 20. *P. illinoense:* Antenna of larva.
Fig. 21. *P. illinoense:* Right mandible of larva in dorsal view.
Fig. 22. *P. illinoense:* Comb at right posterolateral angle of eighth abdominal segment of pupa.
Fig. 23. *Polypedilum sordens:* Left mandible of larva in dorsal view.
Fig. 24. *P. sordens:* Labial plate and right paralabial plate of larva in ventral view.
Fig. 25. *P. sordens:* Antenna of larva.
Fig. 26. *P. sordens:* Comb at right posterolateral angle of eighth abdominal segment of pupa.

THE RELATION OF AMERICAN DRAGONFLY-EATING BIRDS TO THEIR PREY

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THE RELATION OF AMERICAN DRAGONFLY-EATING BIRDS TO THEIR PREY

INTRODUCTION

Twenty-two years ago (1926) the writer was given the privilege of examining the records of the U. S. Biological Survey (now Fish and Wildlife Service) on dragonflies as food of birds. For this opportunity I wish to thank Mr. Waldo L. McAtee who for many years was in charge of the extensive studies of the Biological Survey on bird foods.

Because the writer has not found time to review the Bureau's later collections and bring this paper down to date it is being published now as drafted then because of the great amount of data of that date summarized, data the conclusions from which later investigations have not invalidated. The problems are those of wide food tolerancies, and the necessary contact of bird with dragonfly. Birds eat what is available when pressed by hunger. This view must be held in mind by the reader: conclusions are suggestions: few are critically final.

Extent of the Problem

The present article turns out to be a review of the habits of the water and land birds of America north of Mexico, which concern their use or not of dragonflies as food. The A.(merican) O.(rnithologists') U.(nion) Checklist of North American Birds, Fourth Edition (1931) recognizes 468 named species and subspecies of land and sea birds. The data obtained by the examination of bird stomachs by the then United States Biological Survey showed in 1926 that 184 of the 468 species and subspecies used dragonflies at times. Muttkowski's (1910) Catalogue of the Odonata of North America lists 494 species of dragonflies for a slightly larger continental area, south to parallel 20° N. in Mexico. The present review thus covers a continental bird fauna in its contacts as predators operating against a continental dragonfly fauna. Our summary count shows 61,042 stomachs examined in the 184 species that were found to have eaten dragonflies and that the 184 species of birds (a total of 61,042 individual birds) had captured 2,652 nymphal or adult dragonflies. The reviewer did not copy records of stomachs of bird species that had no dragonfly records against them. This included nearly all sea birds and many land birds, a total of 284 named species and subspecies. Counting all stomachs of sea and land birds the figures suggest that the Survey had examined upwards of 75,000 stomachs by 1925. Cottam & Knappen (1939, p. 138) estimated 200,000 stomachs in the Survey's collection about half of which had been analyzed.

No such mass of expertly gathered data on the problem of predator *versus* prey appears in the literature of the fields of ecology or organic evolution. I wish to comment further: the mass of data has not been gathered by any one man but is that of a staff of some of the most expert ornithologists of recent times who up to 1925 had operated as a changing group over a period of more than forty years (Methods, McAtee 1912).

The accumulated data carries one unavoidable bias: the studies necessarily have been focused on economic species (Beal 1907, 1910), those of value to man and those suspected of being inimical to man's interests. It has been the privilege of a lifetime to review such a mass of expertly gathered data!

The organized study of bird food by the Biological Survey was begun in 1887 and up to 1925 when these notes were abstracted from their files the staff of the Survey had collected and examined the stomachs of many tens of thousands of birds (McAtee 1913). The early history and background of economic ornithology was covered by T. S. Palmer (1900) in one of the most important reviews written on an ornithological subject. At that time the Biological Survey had collected 32,000 bird stomachs. Material piled up faster that it could be numerically invoiced from year to year. Hence we have no published figure on the total of stomachs for 1925. In Palmer's (1900) review it was 32,000 by estimate. This was followed by 26 years of intensive collection and study to the date of this review (1926) (McAtee 1933).

As of interest we wish to call attention to the historic fact that John Ray was the first biologist to open bird stomachs for positive data on bird food (Raven 1942, 327). Also we cite one of the best Scotch papers (Florence 1912) for a comparison of food habits of related palaearctic (Scotch) and nearctic (North American) birds: and Collinge (1924-1927).

Nature of the Records

The Biological Survey records are a card index system arranged according to the A. O. U. Check List which index was begun in the middle eighties of the past century before ornithologists concurred in the recognition of the many subspecies listed in the recent check list. Many of the cards at the time (1926) these notes were abstracted dated from earlier A. O. U. Check Lists (Ed. I, 1886; Ed. II, 1895; Ed. III, 1910). As the birds of the earlier records had not been in many cases identified to a subspecies these records stand as made, usually to the species name only. McAtee has stated to the

writer that "subspecies determinations of birds are unimportant except that birds will eat different species of plants and animals in different floral and faunal areas. That the general nature of bird food is the same in all subspecies of any one bird species." Probably in the succeeding discussion records are listed under the eastern subspecies that at a later date would have been credited to the western or southern subspecies of the same bird. The greater part of the records are of birds shot in the eastern United States.

The Survey studies on the food of birds cover the United States with some records from Alaska, Cuba and Puerto Rico. This article is confined to the Bureau of Biological Survey records with minor additions from literature cited as an outside record in each instance (See Forbes 1882). The writer has followed the American Ornithologists' Union "Check List of North American Birds," Fourth Edition, 1931, in his use of both common and scientific names of birds.

Back of the records on cards is the original collection of the contents of the stomachs that are recorded. These are preserved in alcohol, each stomach contents with its record number.

The earlier work by the Survey was a mere recording of the various kinds of food found in each stomach with the number of items of each when such could be easily counted. In later studies attempts were made to give percentages of the various foods found (Judd 1901, McAtee 1912a, Stevenson 1933). This has been exceedingly difficult as some foods digest so much more rapidly than do others and because percentages are not easily comparable among greatly different kinds of food. In later studies much of the material has been identified to the species of animal or plant used as food. This has involved the assistance of specialists in the different branches of zoology and botany, particularly men familiar with seeds. In insects this means frequently the identification of a beetle from a fragment of elytral sculpturing, a butterfly from an antenna or a leg, a dragonfly from a mandible. Knowing the region from which the bird stomach came, it is surprising how many positive identifications can be made from characters other than those usually used in keys. The writer has done some of this work on fragments of Odonata where frequently only the indigestible mandibles remained. The jaws of Odonata quite often have very specific characters as has been shown recently by Taborsky (1927). For these reasons the present records pertaining to dragonflies as bird food occur roughly in several forms which are not always easily comparable. They may be listed merely as Odonata, sometimes as Anisoptera or Zygoptera or as odonate nymphs or again as Anisoptera nymph or Zygoptera nymph. It will probably be many years before this mass of material can be identified more precisely as it is a very time-consuming process and the present evidence is that such definite identification is hardly warranted. To a bird a dragonfly is either large or small, an adult or a nymph. Only one or two instances, as will be pointed out further on, appear to be more specific. Within the range of their food-habits birds eat whatever is most available (Henderson 1927:59; and personal statement from McAtee). No general attempt was made to identify dragonflies to species to see if brightly colored forms were used more often than dull species. (McAtee 1932.)

The general impression among students of bird foods is that feeding habits are much more plastic than they were supposed to be before the era when students of birds began to examine stomach contents. A few species such as the swifts and bluebirds which at times are killed off by late freezes after they have returned north apparently are less able to make such shifts in food (McAtee 1912b).

It must be remembered that only in studies of abundant economic species, the crow, the English sparrow and such, have stomachs been collected in any number throughout the year. Jenks (1859) made a year-round study of the food of the robin but such studies are few. Thus the greater part of the data, except in a year-round study, is suggestive merely. The Biological Survey had its authority from Congress which was interested in economic species and only in such while they operated in the United States for or against voters (McAtee 1926).

LITERATURE AND DOCUMENTATION

Literature is cited to cover the habits of birds which eat dragonflies and frequently items on close relatives for comparison which do not eat dragonflies as freely. The three most comprehensive works each of which is well indexed and documented are cited by volume only under each family of birds. These are Bent (1919-1946), fourteen volumes, Forbush (1925-1929), three volumes, and Henderson (1927). These quote the work on contents of stomachs down to 1929 and partially (Bent) to 1946. Under each species items from 1929-1947 are cited by the present author less completely. Other useful reviews are Barrows (1912), "Michigan Bird Life," and Warren (1888, 1890), "Birds of Pennsylvania," and McAtee (1913, 1933). Final reference to U.S.D.A. publications is given in "Index to Publications" U.S.D.A. (1932, 1935, 1937, 1943). The extensive literature by the experts of the U. S. Biological Survey (now Fish and Wildlife Service, Chicago 54, Illinois) covered by the preceding general works has formed the heart of the literature studied. The volumes cited give easy reference to this mass of literature plus references to the work of other students in various journals. McAtee (1926), "The role of vertebrates in the control of insect pests" is a good brief review of the general problem with a good bibliography. Strong (1939), a bibliography of birds, was found too "selected." Chapman (1932) is the best review of correlated habits, height and type of nest, ecological distribution, etc. A good European paper Sømme (1933) covers this subject of "Birds as enemies of dragonflies." Tavener (1934) is a good review of food habits of Canadian birds. Allen, Glover M. (1925) is a good general biology of birds.

EXTENT AND POSITION OF ODONATA IN THE ENVIRONMENT

It must be remembered that dragonflies live a dual existence. The greater part of life is spent as a fully aquatic animal in fresh water ponds and streams. Except for a few species which pass the winter in the egg stage (*Lestes* spp.) the nymphs of dragonflies are present in the water at all seasons. The greatest number of *individuals* in the water is probably in the fall when the majority of the eggs laid the previous summer have hatched. Then the ponds and streams are full of small nymphs among which are a smaller number of large nymphs. The nymphs are used as food all fall, winter and early spring by fish, aquatic birds and other aquatic animals. In small ponds that contain no fish dragonfly larvae become very conspicuous by early spring because of numbers and increased size. In waters containing fish they also become more conspicuous because of growth having taken place over winter. Thus in both types of dragonfly water-environment they appear to be a greater part of the total weight of animal life per unit of water in the late spring than at any other season. Late spring, just before the spring emergence, is the best season for collecting nymphs. During the late summer sizable dragonfly nymphs are comparatively scarce except those of fall emerging species. Unfortunately, few or no around-the-year population studies of odonate nymphs appear to have been made. The preceding remarks are the casual observations of a collector. Notice that this seasonal distribution of nymphs of size throws dragonfly nymphs into the "duck season" of spring and fall migrations. Nymphs are less abundant when birds nesting within the limits of the United States are rearing their young. This seasonal distribution of nymphs large enough to be eaten appears to pit the ducks, grebes, etc. directly against dragonflies while in the aquatic stage of life (Kennedy 1928, Knappen 1933, Lyon 1915).

The second part of a dragonfly's life is spent as a land insect on the wing. Though in no sense aquatic except that the majority of flying Odonata live largely on the flying adults of minute species of aquatic Diptera (Warren 1915) and except for a few species that enter the water in oviposition the dragonflies are usually thought of as being mildly aquatic as adults. However, they are aerial land insects as adults. They are on the wing from the first freshet of warm rain water in the spring until the first heavy frost in the fall. Few individuals are probably on the wing more than three weeks (Borror 1934). Unfortunately, Borror's study of adult *Argia moesta* Hagen gives our only data on the length of this phase of life. The majority of species emerge over a short period of time (2-4 weeks?), live on the wing the two to four (?) weeks of adult life and die, apparently of old age (Kennedy 1915). Thus the warm season sees a succession of dragonfly species on the wing among which are scattered a few all-season species. Species on the wing follow in succession as do the flowers of the woods and fields. It is this seasonal succession (Kennedy 1928, Walker 1915) of aerial forms which are available as food to land birds. *But* they have to be birds which for one reason or another are associated with the aquatic dragonfly habitat. Dragonflies as a rule do not stray far from the water. They oviposit in or close to the water and usually use minute Diptera as food. Immatures of the latter are usually aquatic or live as larvae in the very wet ground bordering ponds and streams.

Odonata are exposed to both water and land birds at another time of life. This is during the few hours when the nymphs crawl out of water, the back splits open, the adults emerge from the nymphal skin and sit around flabby and helpless until wings and skeleton harden. While the crawling out of the water and the stripping off of the nymphal exuvium may occupy less than an hour, hardening with full color comes slowly. Frequently almost the whole of daylight is occupied in this change before the dragonfly can fly speedily. During this helpless stage dragonflies are fed upon by aquatic birds, grebes, nesting ducks, herons, etc. and by land birds, those species that search beaches and hunt in emergent aquatic vegetation, such as the yellow-headed blackbirds, western robins, marsh wrens, etc.

It must be remembered that dragonflies, while they may appear abundant in narrow areas because of their intense activity, bright colors, and rather large size, are actually seldom abundant as compared with herbivorous insects. On small streams where a species seemed abundant the writer (1915) has appeared to have been able to catch the majority of flying individuals on a mile of stream in four or five days' collecting. The total number of individuals taken, which, with their continuous activity, gave the impression of great abundance, might be twenty-five or might, with some other species, be one hundred or even two hundred, but after the four or five days' collecting they had dwindled to stray individuals only. For a mile or two of habitat even two hundred is a very small population of insects. Along the banks of the same stream might be from one hundred to one thousand ant nests, each of which would house twenty to several thousand ants. The activity, bright colors and size make dragonflies appear many times more numerous than they really are.

Dragonflies are predatory insects and occupy the same niche in the insect world as that occupied by hawks and owls in the bird world. They are at the peak of a pyramid of numbers (Elton 1935). As adults they feed on midges which as dragonfly food are many more times as abundant as the predator dragonfly species. The midges as larvae feed on yet smaller aquatic organisms, but more abundant than the midge species. This lowest level of the animal part of the pyramid of numbers the apex of which forms the food of dragonfly adults feeds on algae, large Protozoa, and perhaps dead organic matter, a still more extensive body of food. Thus being at the apex of a pyramid of numbers Odonata cannot be

enough to furnish a continuous (in time) supply of food to some other predator (in the instance of our study, birds). Dragonflies are rather exceptional insects in the environment when compared with the hemipteroid orders, the beetles, the flies and the world of ants and other hymenopterous insects. Except for an occasional local swarm, an event so rare that, if observed, it is recorded in the literature, dragonflies are never as abundant as are herbivorous insects. These conditions prevent them from ever becoming the regular food of any species of bird at our latitude, with the possible exception of the larger swallows and martins and as food for nestlings; (Franklin's gull the yellow-headed blackbird, purple martin—see Judd (1901).

BIRDS WHICH ONLY ACCIDENTALLY OR NEVER EAT DRAGONFLIES

Of the seventy-five families of birds of the United States about forty families do not eat dragonflies. Many of these exceptions are obvious but others are less so, and some must eat dragonflies at times though the present records have no data in that regard.

All of the birds of the open sea and the rocky foreshores of the ocean, birds that feed largely on fish, Crustacea or marine worms have usually no records against them. Dragonflies are insects of fresh water and, as has been shown by Osburn (1906), nymphs of various fresh water species cannot stand a concentration of sea salts of more than 11% of that of the open sea. In warmer regions than Woods Hole, where Osburn conducted his experiments, are various species of brackish water dragonflies that appear to be able to stand a greater concentration. A few such were studied by Pearse (1932) in brackish pools on Dry Tortugas where salinity was as high as 67% of that of sea water. Nymphs of ***Erythrodiplax berenice*** Drury and ***Ischnura ramburii*** Selys appeared to stand this high salinity. However, there are very few species of brackish water Odonata and these are usually found about waters of much lower salinity. Sea birds on this account do not come into contact with dragonflies but live in a separate saline environment. This appears in the records of the Biological Survey.

The writer includes in this list of sea birds the following families: Gaviidae (Loons, some spp.); Diomedeidae (albatrosses); Procellariidae (shearwaters); Hydrobatidae (storm petrels); Phaëthontidae (tropic birds); Pelecanidae (Pelicans, some spp.); Sulidae (gannets and boobies); Phalacrocoracidae (Cormorants, some spp.); Fregatidae (man-o'war-birds); Phoenicopteridae (flamingos, some colonies); Haematopodidae (oyster-catcher); Stercorariidae (jaegers); Laridae (gulls, some spp.); Rynchopidae (skimmers); Alcidae (auks and murres).

This is an interesting series of families as nearly all of them are rated low in bird evolution. Probably in their earlier evolution they had relatives on inland waters but these were exterminated in the late Mesozoic or early Tertiary with the rise of small carnivorous mammals. These birds usually nest in colonies and on the ground or in cliffs where small carnivorous mammals could easily exterminate whole colonies if they could get to their nesting grounds. Now they are limited to isolated islands, outlying bars and beetling cliffs which types of surface occur more often along sea shores because of tidal currents and the greater waves of storms. Further, their young develop slowly so that the family has a long period when exposure to ground vermin would be disastrous. Their few relatives that are colonial, gulls, terns, herons, etc., and which still exist around fresh waters have managed to build their nests away from continuous ground which would give an approach to beasts of prey.

Variously related to the preceding group of sea birds is a series of fresh water families that have managed to occupy the larger bodies of inland waters and coastal bays, swamps and estuaries. These are the following: Gaviidae (loons, some spp.) nesting on the edge of lakes; Pelecanidae (pelicans, some spp.) nesting on islands in sounds and western salt lakes; Phalacrocoracidae (cormorants, some spp.) nesting in trees and on cliffs, living on coastal lakes and coastal islands; Anhingidae (darters) nesting in trees in swamps; Ciconiidae (wood ibis) nesting in trees; Threskiornithidae (true ibises) nesting on islands; the Cygninae (swans) and the Anserinae (geese, brants) of the Anatidae nesting in wet marshes or on islands.

With the exception of the geese and swans which are vegetarian, the flamingos which feed largely on mollusks, and the wood ibis, these are largely fish eaters. Their specialized food habits eliminate dragonflies from their diet. It is interesting that the ducks which use a mixed diet and some of which eat dragonfly nymphs have in their close relatives, the geese, a group of species so wholly vegetarian that they never eat dragonflies.

To this group of families should be added the Rallidae (rails, gallinules, coots). These live in the very midst of the best dragonfly habitats but with the exception of the coot there are no stomach records showing dragonflies as food. Thus the geese and rails, while living in a dragonfly environment, appear to make little use of dragonflies as food. They are two groups of birds that would have been expected to have used them more.

Our next series of families are land birds that for various reasons do not eat Odonata. The usual reason is food preference but in other cases the environment of bird and dragonfly may not coincide or the seasons of occurrence of the bird in the area of the United States may not coincide with the flight season of dragonflies as in the case of northern birds wintering in this area.

This series of land birds which do not eat dragonflies includes the following forms that feed on the ground; Cathartidae (vultures); Tetraonidae (grouse, ptarmigan, sage hen, etc.); Perdicidae (quails); Phasianidae (pheasants); Columbidae (pigeons, doves); Alaudidae (larks).

The three gallinaceous families, while notorious

feeders on insects, are upland groups where dragonflies are seldom found. They live on large slow insects which type of food with the component of seeds and grains is associated with slow movement, poor monocular vision and relatively short necks. The doves and pigeons are herbivores and live largely on nuts, seeds and grains. The vultures are carrion eaters. The larks, while using a small amount of insects in the summer, are largely feeders on seeds and also occupy upland areas where dragonflies are not found. An exception in this series is the family Meleagridae (turkeys). Of nineteen stomachs examined one contained a dragonfly. The turkeys are feeders on insects as well as grains and seeds and in many regions, particularly in the south, are inhabitants of swamps where Odonata abound. In such places where taste, bird and dragonfly coincide they probably eat dragonfles more often than the Survey records show.

Among the birds of prey the Pandioninae (ospreys) and the Tytonidae (barn owls) have no records of using dragonflies as food. The first eat fish while the barn owls feed at night when dragonflies are not on the wing. The barn owl lives almost entirely on small mammals and is one of the most highly specialized owls. Being more highly owl-like it is more strictly nocturnal than the other American owls which occasionally catch dragonflies at dusk. In its time of flight it is further from the time of flight of the diurnal Odonata.

The eagles, Buteoninae, and other large hawks of the Accipitriidae do not use dragonflies. They are usually interested in larger prey.

Among the tree-inhabiting and perching birds a few families show no records of stomachs with dragonflies. These are the Trochilidae (hummingbirds) which live on minute insects and nectar; Motacillidae (wagtails, pipits) which feed on insects and seeds but feed on high open ground where dragonflies seldom occur; Certhiidae (creepers) and Sittidae (nuthatches) which search tree trunks for minute insects and the Sylviidae (kinglets, gnatcatchers) which live on minute insects. The kinglets winter in the States when dragonflies are not on the wing but the family is represented in the western states by four species of gnatcatchers, one of which, the blue-gray gnatcatcher, extends to the Atlantic coast, which do not eat Odonata perhaps because of their diminutive stature and very small beaks.

Thus birds that do not eat Odonata are checked by one or more of the following factors:

1. They have a special food preference that does not include dragonflies as for example the osprey, a fish eater; the flamingo, a mollusk eater (Chapman 1905); the vultures, carrion eaters.

2. They may have a habitat that does not include dragonflies as for example the sea birds, the quails, grouse, pipits, larks, which inhabit high dry areas and the nuthatches which seldom leave the trunks and limbs of the larger trees.

3. They may be mere winter visitors in the United States when dragonflies are not on the wing but probably do eat dragonflies on their nesting grounds as for example the northern blue bird and the bohemian wax-wing.

4. They may be so deeply nocturnal that their time of flight does not coincide with even the crepuscular Odonata, thus by time of day being out of the dragonfly habitat, as for possible example, the barn-owl.

5. They may be so large that they ignore insects as food though their smaller relatives use them plentifully as for instance the eagles.

6. They may be so small that they show a distinct preference for minute insects, as example the gnatcatchers and the humming birds.

7. While feeding on the ground they may be so slow in reaction time, so short-necked and with such poor vision, monocular, that dragonfly adults are too fast for them. Examples are rails and perhaps turkeys.

8. A few birds have bills so specialized for specific foods accompanied by tastes for diets which do not include insects that the shape of the bill prevents use of the bill for insects. Examples are the flamingo (Phoenicopteridae), a mollusk-eater, and the oystercatcher (Haematopodidae) with its chisel used on bivalves. Uusally the problem is not as simple as listed. In the skimmers (Rynchopidae) the bill is specialized but the skimmers in being wholly marine are already out of dragonfly environment.

BIRDS WHICH EAT DRAGONFLIES

EGGS OF ODONATA EATEN ONLY ACCIDENTALLY

Apparently dragonflies while in the egg stage are not regularly attacked by birds. Some plant-eating waterfowl may take such occasionally (the eggs of Zygoptera) while feeding on floating aquatic plants but few birds feed on floating plants, those large and tough enough to interest an ovipositing female dragonfly. Dragonfly eggs are oviposited in three or four ways. The Libellulidae and Gomphidae wash them off the vulvar parts by touching the abdomen to the surface of the water. The eggs usually float apart almost immediately and drop to the bottom. However, the Cordulidae lay eggs, as do toads and frogs, in masses of gelatinous envelope, usually gelatinous strings of eggs festooned over submerged vegetation. We have no records that birds eat these, but the facts have never been sought out. A few dragonflies with a large shovel-like ovipositer (Cordulagesteridae, and occasional species of Libellulidae) oviposit by thrusting eggs into mud or stream bottom. The majority of the Zygoptera oviposit endophytically, as also do the Aeshnidae. Here with a sharp, hard, needle-like ovipositor the eggs are placed deep into plant tissue, less often in crevices of mossy rock as laid by *Aeshna walkeri* Kennedy (1917).

The birds which take *insect* eggs as a regular part of the diet are largely the smaller tree-inhabiting land species, insectivorous forms that search the bark, twigs and leaves of forest shrubs and trees. Some such are titmice, wood warblers, vireos, nuthatches,

brown creeper, the smaller woodpeckers, etc. These egg hunters seldom enter the environment where dragonfly eggs are deposited. Only one North American dragonfly (*Archilestes californica* McL.) is known which oviposits in trees (willow; Kennedy 1915).

BIRDS TAKE NYMPHS AND ADULTS AT A DISADVANTAGE

The few species of birds that use dragonflies to any considerable extent as food take the dragonfly at a disadvantage. Several such types of advantage of bird predator over dragonfly as prey can be pointed out.

1. The bird may scoop the dragonfly nymph up with a shoveling bill as do the ducks when the nymph is burrowing in the mud, sand or trash at the bottom of a pond or stream. This is particularly a habit of feeding among the river ducks of which the Shoveller Duck is the outstanding example. This type of capture is especially destructive to dragonflies during the cooler parts of the year when the nymphs of many species of dragonflies drop to the bottom in a sluggish condition, a form of hibernation or semi-hibernation. The American avocet hunts with its upturned bill in somewhat the same manner.

2. Some species of birds take great numbers of dragonflies when nymphs crawl out of the water in the process of the emergence of the winged land adult from the skin of the aquatic nymph, which process has to be completed in the air. The dragonfly is at a great disadvantage at this time in two ways. First the nymph is not a land animal yet has to crawl some distance on land sometimes a hundred or more feet (Cordulinae). It is slow and awkward with no protection except perhaps a lack of bright color to the bird eye. Second, it is in a physiological condition which reduces its behavior, its reactions to dangers of the environment, to their lowest point in its life cycle beyond the egg stage. This low physiological condition continues for some hours until the wings are fully expanded, fully hardened and until after trial flights have been taken and the neuromuscular apparatus has turned up. It probably involves a meal or two before the imago is at top imaginal speed in its reactions to the dangers surrounding it. The species of birds that appear the heaviest feeders on Odonata at emergence are the martin, yellow-headed blackbird, the western robin, and Franklin gull (Gould 1871).

3. Birds that hunt in emergent vegetation, taking adult Zygoptera particularly, find the dragonfly at a disadvantage because of the slow flight of the latter necessary in dodging between the upright sedges, cattails, etc. Dragonflies are very slow in flight under such conditions. Here we were surprised to find that the rails did not get many Odonata. The American bittern, least bittern, and green heron excel in taking dragonflies in this type of disadvantage to the latter. The standing position of the immobile bittern with its bill pointed straight up could be a position useful in catching dragonflies flying over as well as a position of concealment, its usual interpretation.

4. Birds that fly as well or better than do dragonflies have dragonflies at a disadvantage not only in ability on the wing but because the bird has clearer eyesight. The dragonfly depends on mosaic vision (Exner 1891), which is dim with hazy outlines at best though it may define a moving object (enemy or prey) fairly well. The flying predator bird has the most highly developed eyes known in the animal kingdom and so must have a very fine vision. Such take many flying Odonata. Examples are the martins and the smaller falcons.

5. Dragonflies rest on tree trunks as well as on smaller plants when too cool for flight. This habit may account for Odonata found in woodpecker stomachs especially in yellow-bellied sapsucker stomachs. Also some dragonflies cease flight at 105° F. or higher when they rest as if too cold (Walker 1912).

6. Vast numbers of dragonflies are stranded as nymphs in ephemeral shallow pools each season. When found by birds they may account for the occasional bird stomach containing 10 to 30 nymphs in a series where other stomachs contained one or two.

DRAGONFLIES AS FOOD OF NESTLINGS

Little manual stomach examination has been done on nestling birds. (The literature on observation by field glass has not been reviewed.) Discussion of the following cases will be found under the names of the species to which attention is directed here. The Franklin gull, a bird of northern mid-American marsh-bordered lakes, was found by Roberts to be feeding its nestlings on dragonfly nymphs. This gull is almost wholly insectivorous state McAtee and Beal (1924).

The purple martin has been found by Beal (1918) to feed its young on Odonata. See also Doolittle (1919). This bird prefers nest boxes near water. The yellow-headed blackbird which nests in the cattail swamps of the western states feeds its nestlings on teneral aquatic insects a high percentage of which are dragonflies. (See Fautin (1940) for a bibliography: see this article, northern crested flycatcher; Franklin's gull; western robin; marsh wrens. See Judd 1901).

COMPETITION FOR FOOD BETWEEN BIRDS AND DRAGONFLIES

Few birds compete directly with dragonflies for food which may be common to both. In the water, food common to both would include the smaller aquatic animals and on land largely the minute dipters (Campion 1914, 1921; Lyon 1915; Warren, Alfred, 1915). In the water, ducks take aquatic animals but usually those larger than would be attacked, except perhaps by the largest aeshnine numphs. On land there are few insectivorous birds which use small insects and which also fly regularly about streams. Some of the flycatchers live near streams and some of the smaller of these take many small insects. But the greater number of insectivorous birds that are small enough to be interested in the insects which are small enough (gnats) to interest the average dragonfly, are arboreal birds largely restricted to

timber. The possible competitors with flying Odonata for minute insects are such birds as humming birds, titmice, warblers, kinglets, vireos, some small fly-catchers, etc. which seldom hunt near streams. (See early notes by Poulton 1906.)

THE UNITED STATES FISH AND WILDLIFE SERVICE'S DATA ON BIRD STOMACH CONTENTS. NOTES ON FOOD PREFERENCES AND HABITS WHICH CONTACT BIRD AND DRAGONFLY

FAMILY COLYMBIDAE (grebes)

The lowest order in the United States bird fauna (the members of which catch dragonflies) is the Order Colymbiformes which, in our area, includes the single family of the grebes. These are as thoroughly aquatic as any of our fresh-water birds and are remarkable for their great speed of muscular reaction.

With this speed of movement is associated a remarkable acuteness of vision. The retina of the eye is provided with a highly developed monocular (nasal) fovea which consists of the usual pit-like fovea but extending from it to the nasal edge of the retina is a fossa, probably an extension of the area of acute vision that gives the grebe the ability to see objects distinctly which lie to one side (monocular vision) but actually back of the grebe's position. Thus the grebe is very sensitively keyed to his environment by a remarkable range of acute vision. Apparently, the grebe does not have the acute binocular vision as do birds that on the wing strike prey, such as the owls, hawks, swallows, humming birds and others which usually have a well developed temporal fovea used binocularly. The foveae of the great crested grebe of Europe, *Podiceps cristatus* (Linnaeus), are figured (Fig. 121, p. 72) by Doctor Casey Wood (1917) on bird eyes. Compare Fig. 121 with the retina of doves and pigeons (Wood 1917, Figs. 118 and 119) which eat seeds, nuts and fruit, and whose retinas have no highly developed areas of acute vision.

The grebes are birds of swamps, ponds, and the edges of freshwater lakes. Nests are built on floating rafts of cattails in the outer edge of emergent vegetation which supports the densest population of dragonflies. The food of all species is about 100% animal substances including fish, worms, Crustacea, and insects. All species have a curious habit of eating their own feathers so that grebe stomachs usually contains balls of feathers. The following are monographic and apply to the species of grebes cited, Bent (1919), Forbush (1925), Henderson (1927), McAtee & Beal (1912, 1924), Munro (1941), Wetmore (1924).

Holboell Grebe, *Colymbus grisegena holboelli* (Reinhardt): 50 stomachs examined, one with several adult dragonflies. About 50% of the stomach contents, other than feathers, of the Holboell grebe is fish, often with crustaceans as high as 20%, the remainder being aquatic insects.

Horned Grebe, *Colymbus auritus* L.: 156 stomachs examined, 3 with libelluline nymphs and 3 with adult Odonata. In a third of the stomachs fish ran to about 35% and crustacea 7-10%.

Eared Grebe, *Colymbus nigricollis californicus* (Heermann): 35 stomachs examined, 6 with odonate nymphs and 1 with specimens of *Enallagma* sp., an adult Zygoptera. Less than 20% of the food of the eared grebe is rated as fish, the remainder being crustaceans, worms, and insects.

Pied-billed Grebe, *Podilymbus podiceps podiceps* (L.): 196 stomachs examined, 23 with Odonata. Of these 10 contained aeshnine nymphs, one a libelluline nymph, one a zygopterous nymph, 6 unplaced "odonate nymphs" and 4 adult dragonflies. The food of this bird averaged 24% fish, 27% crayfish with the remainder largely aquatic insects. According to Wetmore (1924) some of the stomachs contained adult Zygoptera up to 8-34% of the total food.

Antillean Grebe, *Podilymbus podiceps antillarum* Bangs: One Puerto Rican stomach contained 2 dragonflies and 25 crayfish (Wetmore 1916).

At the same low evolutionary level as the Order Colymbiformes (Grebes) are three other orders of aquatic fowl. One order, the Gaviiformes (Loons) are fresh water as well as salt water in habit and while living largely on small fish eat insects, crustacea, leeches, amphibians, etc. Probably loons at times take dragonfly nymphs though the Survey's records contain no such records. The other two orders, the Procellariiformes (albatrosses, shearwaters, petrels) are marine while the Pelicaniformes (pelicans, cormorants, darters, etc.) are salt water fowl generally with a few exceptions on salt lakes and estuaries. The darters, found in semitropical swamps, may at times take Odonata as insects are recorded in their stomachs. The other families of these orders are outside the fresh water environment of dragonflies.

The succeeding orders of birds tend towards a fresh water or land habitat and in the sixteen orders to follow only two, the Columbiformes (doves and pigeons) and the Trogoniformes (trogons), a tropical group, have no records whatever of having eaten Odonata. This brings us to the first family of this series of fresh water and land birds.

FAMILY ARDEIDAE (herons, egrets, bitterns)

In this series of families which compose the Order Ciconiiformes are the ibises, storks, bitterns, cranes and herons where we come into a series of birds which feed on a wide group of moving animals. With this preference for moving prey is the fact of their life about the shores of fresh waters where dragonflies are most abundant and the further factor that the majority of species are of that intermediate size among birds which is associated with the capture of dragonflies. The positive combination of food habit or preference, of living in a dragonfly environment and of size of bird in relation to food eaten shows at once in the large number of Odonata eaten by most members of the Order Ciconiiformes.

Casey Wood (1917) shows that the Ciconiiformes have besides the usual nasal fovea for monocular

vision a well developed temporal fovea or area of acute vision on the outer rim of the retina which indicates an acute binocular vision. This type of eye is found widely in birds that take moving prey. It permits accurate and speedy bill work. Further the long legs of this group permit wading in the shallow vegetation-filled waters where, because of vegetation, swimming is more difficult than in open water. Here dragonflies are the most abundant. The long neck in these birds gives range in striking prey. All the species of the Ardeidae probably eat dragonflies regularly, both in the nymphal and in the adult form.

However nine species of this family found within our area have no records of having eaten Odonata. The herons are a group of birds that live in the very midst of the most densely populated dragonfly habitat and eat any small, moving vertebrate, crustacean or large insect. Some species, notably the green heron, catch more adult Odonata than nymphs. The latter species lives along wooded streams where dragonflies fly more slowly on account of the vegetation than they do over more open water which may account for the greater proportion of adults in their food.

Birds of this family feed while standing on their feet. Compare their records with marsh-inhabiting Passeriformes of the same general insectivorous tastes but perhaps of a slightly smaller order of size such as the red-winged blackbirds. The heron-like birds have the distinct advantage of a long neck in obtaining active insects. As we shall see, the birds that feed standing and that have short necks use slow insects, Orthoptera, Coleoptera, Hemiptera, caterpillars, etc. (Bent 1927; Baynard 1912; Forbush 1925; Henderson 1927; Wetmore 1916).

Great Blue Heron, *Ardea herodias herodias* L.: 125 stomachs examined, 29 containing Odonata, 19 of which were adults and 12 of which were identified as adult Anisoptera. The usual articles of diet of this bird are fish, frogs and crayfish, but it takes almost any animal, including snakes, salamanders, mice, gophers and large insects including locusts.

(The American Egret, *Casmerodius albus egretta* (Gmelin) appears to use a diet of animals from the higher meadows and is a larger bird. This may explain the lack of Odonata in the stomachs examined by the Survey.)

Snowy Egret, *Egretta thula thula* (Molina): 20 stomachs examined, 5 of which contained dragonfly adults. Other published records indicate that it also eats nymphs. It is a bird of brackish waters and low, marshy meadows, feeding on crayfish, fish, and swimming aquatic insects.

Louisiana Heron, *Hydranassa tricolor ruficollis* (Gosse): 60 stomachs examined, 10 with dragonflies, 9 of which were adults: Food similar to the preceding egret but taking many top-minnows and grasshoppers.

Little Blue Heron, *Florida caerulea caerulea* (L.): 45 stomachs examined, 27 with dragonflies, 7 of which were adults. One stomach contained 18 and another 31 nymphs. Evidently dragonfly nymphs are a regular item of diet. This is a bird of more open waters than the next, the Green Heron, and the records show its food to be fish, frogs, crustaceans, and swimming insects.

Green Heron, *Butorides virescens virescens* (L.): 215 stomachs examined, 80 with dragonflies, 59 of which were adults and the majority of these Anisoptera. Several of the stomachs, 23 in all, contained 2 or more and 8 stomachs contained from 5 to 33 dragonflies. This is a bird, solitary in habit, living on small streams and in wooded swamps where it eats a diet of the usual heron type but of noticeably large forms including snakes, lizards and amphibians though it is the smallest heron, excepting the least bittern. However, it has a heavy short beak which may help it manage food large for the size of the bird. It catches more adult insects, including caddis flies, grasshoppers, etc., than do the other herons. (Bowdish 1903; Warburton 1948).

Black-crowned Night Heron, *Nycticorax nycticorax hoactli* (Gmelin): 100 stomachs examined, 12 with dragonflies of which 5 were adults. This heron eats fish usually but takes also amphibians, crayfish and miscellaneous aquatic insects.

Yellow-crowned Night Heron, *Nyctanassa violacea violacea* (L.): 110 stomachs examined, 1 with a dragonfly. This bird eats fish, crustaceans and worms. The two night herons are puzzles. Both are crepuscular as well as nocturnal. Bent considers the yellow-crowned more nearly diurnal but in 110 stomachs it has only 1 dragonfly. Habits are poorly known of either species. (Howell, A. H., 1924.)

American Bittern, *Botaurus lentiginosus* (Montagu): 125 stomachs examined, 29 containing dragonflies, 17 of which were adults. The speed of this bird in striking prey as it stands concealed amidst swarming dragonflies helps to account for these in its food. It eats also fish, frogs, crayfish, aquatic insects and marsh Orthoptera (Gabrielson 1914).

Least Bittern, *Ixobrychus exilis exilis* (Gmelin): 100 stomachs examined, 41 with dragonflies, 16 of which were adults. From the Survey records the food of this bird includes many small fish and submerged aquatic insects including Coricidae, Belastomidae, and Notonectidae. The records indicate that it catches Odonata twice as often as does its large relative, the American bittern. This is the same relationship of size of bird to size of food as will be noted in the ducks where the small ducks take dragonflies oftener than do the large ducks. We will see the same relationship in the hawks, owls and crows. Two possible explanations occur, one, that the larger birds are able to use larger animals as food and prefer to do so, the other that the larger birds more often occupy more open water including the sea and its bays while the smaller species live in the protection of vegetation about shallower waters where Odonata are abundant. Few published records of food of the least bittern; Sutton (1936).

FAMILY THRESKIORNITHIDAE (true ibises)

The ibises are birds of the fresh water marshes and wet prairies living on crayfish, small snakes, grasshoppers, and other large insects. The series of animals eaten by them suggests that they capture those which are slower and more easily taken than are adult Odonata and that, excepting crayfish which at times form a large item, and a few aquatic beetles, they live mostly on sedentary aerial marsh animals. If actually slow, this accounts for the few adult Odonata taken and their lack of interest in fully aquatic forms accounts for the lack of nymphs in their food.

Wood's (1917) study shows that the true ibises have only a nasal fovea hence only monocular vision. As compared with the herons which have both monocular and binocular vision they capture only nymphs and *may* take these only when stranded in drying pools (Bent 1927; Forbush 1925; Henderson 1927).

White-faced Glossy Ibis, *Plegadis guarauna* (L.): 15 stomachs examined, one stomach with 22 zygopterous nymphs and one with 2 nymphs. The single published record discloses a single stomach containing aquatic plants and one beetle.

There are no records against the Glossy Ibis as an eater of Odonata (Baynard 1913).

White Ibis, *Gaura alba* (L.): 20 stomachs examined, one with an anisopterous nymph. Baynard's (1912) reports on food given young in nest lists crayfish as the largest item with cutworms, grasshoppers, and snakes.

(Rated as a subfamily of the true ibises are the spoonbills. The group is represented in the area of this study by the one species, the roseate spoonbill, *Ajaia ajaia* (L.). Little is known concerning its food. It lives in shallow fresh waters and feeds by emersing the bill and swinging it from side to side in search of food. By such indiscriminate feeding it probably takes dragonfly nymphs at times.)

(In the Order Ciconiiformes are two families against which there are no records of having eaten Odonata. The storks (Ciconiidae) are represented in our fauna by the wood ibis (*Mycteria americana* L.) which has only monocular vision (Wood 1917) and has food habits similar to those of the true ibises (Henderson 1927).)

(The flamingos (Phoenicopteridae), the other family, have been set out under our division of birds that do not eat Odonata because of their salt water habitat and taste for mollusks (Chapman 1905).)

The next order as rated in the A. O. U. Check List, 1931, is that of the Ansereformes which includes the geese, swans and ducks. This order tends towards more vegetable matter in the food which in the geese and swans becomes almost 100 per cent. As shown by Casey Wood (1917), the species of this order have only moderately acute monocular vision. All species have a nasal fovea and in some, the area of acute vision is extended on either side of the fovea in a narrow band. The taste for animal food on the part of the ducks and their use of the same environment as that used by odonate nymphs makes them active enemies of nymphal Odonata.

FAMILY ANATIDAE (ducks, geese, swans)

Excepting the sea ducks, the Anatidae live in the most abundantly populated dragonfly habitats. They are feeders on insects along with other animal and vegetable matter. They obtain their food by swimming or diving, so are constantly brought into contact with either nymphs or adults of dragonflies or both. Hence as a group, the ducks are consistently dragonfly eaters. But as in any large group of species, tastes and habits vary from species to species so that some prey oftener on dragonflies than do others. The group falls into two major series, (1) the geese, brants and swans and (2) the ducks (Munro 1940, 1943, 1944).

The ducks proper fall into three series: (1) the river ducks which live in a rich dragonfly environment and consume many such; (2) the sea ducks, the smaller species of which are the only ones which enter inland shallow waters and use dragonflies; and (3) the mergansers or fish ducks with toothed raptorial bills which variously occupy inland waters and in dragonfly waters use dragonfly nymphs as an item of food.

The River Ducks: In this series the bill is broad and is usually used to shovel mud from pond or stream bottom with bird up-ended or diving. The mud is sifted out through the fluted sides of the bill while morsels of food are retained. These catch burrowing nymphs and nymphs hibernating on the bottom (Bent 1923; Cottam 1939; Forbush 1925; Henderson 1927; Munro 1944).

Mallard Duck, *Anas platyrhynchos platyrhynchos* L.: 2,010 stomachs examined of which 197 contained remains of dragonflies. 126 records are of nymphs of which only 6 are zygopterous. Of the 71 stomachs with adults only 8 were zygopterous, but one stomach contained 7 and another 40 Enallagmas. Thus the mallard tends to use large dragonflies, whether nymphs or adults. The food of the mallard is 90% vegetable. The animal food of the mallard is about 10% of the whole, one-fourth of which is insects, one-half mollusks and the other fourth crustaceans and miscellaneous matter (McAtee 1918; Munro 1943, 1944).

Black Duck, *Anas rubripes tristis* Brewster: 645 stomachs examined, 25 with dragonflies of which only 5 were adults. The food of the black duck is about 75% vegetable, 12% mollusks, 8% crustaceans and 5% insects, fish and miscellaneous. Habits similar to those of the mallard but feeds more often on salt water where Odonata do not occur.

Southern Black Duck, Florida Duck, *Anas fulvigula fulvigula* Ridgway: 52 stomachs examined, 10 with Odonata of which only 4 were adults. While this duck rates as a brackish water duck it is resident on the Gulf Coast the year around and being in a con-

tinuous dragonfly habitat apparently catches these oftener than do the mallard and the black ducks, close relatives. Its food is 60% vegetable matter, mollusks 27%, insects 9%.

Gray Duck, Gadwall, *Chaulelasmus streperus* (L.): 410 stomachs examined, 5 containing Odonata of which only 2 were adults. The gadwall's food is 98% vegetable, insects ½% and mollusks 1.6%. The gadwall is a surface feeding duck but can dive in escape.

Baldpate, American Widgeon, *Mareca americana* (Gmelin): 270 stomachs examined, 2 with dragonflies of which one was an adult. The food is 96% vegetable matter, ½% insects and 6/25% mollusks. The baldpate is a surface feeder tending to the parasitic habit of stealing food from diving ducks. This habit raises the percentage of vegetable food.

Pintail Duck, *Dafila acuta tzisihoa* (Vieillot): 925 stomachs examined, 35 with dragonflies of which 28 were nymphs, 2 only of the latter being Zygoptera. The food is 87% vegetable, insects 2.8%, mollusks 5.8% and crustaceans 3.7%. This is probably the speediest and most active of the ducks but shows *no greater catch* of adult dragonflies than do the slower species. This super-duck which jumps into the air, not having to run on water to rise, and which has a circumpolar distribution tends to feed on shore lines where dragonfly larvae are few. It feeds just outside by a few feet of the winter habitat of odonate nymphs. Its great agility does not increase its intake of Odonata (Munro 1944).

Green-winged Teal, *Nettion carolinense* (Gmelin): 750 stomachs examined, 27 with dragonflies of which 18 records were of nymphs. The food of this species is 90% vegetable, insects, 4.5%, mollusks 4%. The 30% of adult Odonata are probably due to its habit of wading in shallow water during nesting season and to its well known speed in action: one of the speediest.

Blue-winged Teal, *Querquedula discors* (L.): 335 stomachs examined, 27 with Odonata, 6 of which contained adults. The food is 70% vegetable, insects 10%, mollusks 17%. The blue-winged teal comes south in late summer which accounts for adult dragonflies. It occupies marsh ponds, shallow waters and shore lines, has the speed of reaction found in the green-winged teal, which accounts for the greater number of Odonata.

Cinnamon Teal, *Querquedula cyanoptera* (Vieillot): 44 stomachs examined, 4 with dragonflies all of which were adults. This is a western species breeding in the densely populated dragonfly habitats about western ponds and marshes. Unfortunately, the published records are of eastern individuals strayed from their natural habitats, or may be misidentifications. Vegetable food, 80%, insects 10%, mollusks 8%.

Shoveller Duck, Spoon Bill Duck, *Spatula clypeata* (L.): 88 stomachs examined, 3 with Odonata of which 2 were nymphs. Vegetable matter 65%, mollusks 18%, insects, small fishes 3%. The shoveller duck is built to feed by sifting mud through its highly specialized bill so that its take of nymphs is purely accidental. However, McAtee (1922) states that much of its food is obviously taken without such sifting of the bottom mud.

Wood Duck, *Aix sponsa* (L.): 400 stomachs examined, 78 containing dragonflies, of which 56 were nymphs, the majority being Anisoptera. Of the total food, 90% is vegetable, insects 6.3%, spiders, mites and crustaceans 1%; no mollusks taken. McAtee's figures for the wood duck are, vegetable food 10%, dragonflies and nymphs 2.5%, bugs 1.56%, beetles 1.02%, Orthoptera .23%. He found that in 16 stomachs taken in March 1.75% of the food consisted of dragonflies the majority of which were nymphs, of 9 taken in April, 10.44% was dragonflies, mostly nymphs. This rise in the number of nymphs taken during the early spring was found also in the southern black duck and is accounted for by the fact that odonate larvae are then full grown and are awaiting for the late spring emergence. They are then large enough to be taken by a duck and their numbers have not been depleted by emergence. Warren (1888) records seeds including acorns and calls it "Summer Duck, Wood Duck, Acorn Duck."

This ends the series of river ducks all of which use dragonflies to some extent.

The Sea Ducks or Diving Ducks: The following are called sea ducks and live on more open and deeper waters where there are fewer opportunities to capture dragonflies. Of the 18 species of sea ducks 10 have no records of having used dragonflies as food. These are the eiders and other ducks of the sea coast and more open bays and estuaries, the majority of which are vigorous, active ducks that do not seek the protection of shallow, weedy waters. However, three of the smaller species of this group do not venture into open waters. They feed about in shallow waters, and rate high as eaters of dragonflies. These are the blue-bill, ring-necked and bufflehead ducks (Bent 1923, 1925; Cottam 1933, 1939—best bibliography; Forbush 1925; Henderson 1927).

Redhead Duck, *Nyroca americana* (Eyton): 360 stomachs examined, 10 with dragonflies only one of which was a nymph. No thorough analysis of the food of this duck has been published (1925). It is a heavy eater of vegetable matter but takes also fish, amphibians, mollusks, and a few insects.

Ring-necked Duck, *Nyroca collaris* (Donovan): 655 stomachs examined, 92 with Odonata, 84 of which were adults. This is another small Nyroca and according to Bent the greater part of its food is vegetable but it takes a scattering of insects. It is more of a fresh water duck than the other Nyrocas and thus comes more often into the dragonfly habitat.

Canvasback Duck, *Nyroca valisineria* (Wilson): 380 stomachs examined, 10 with dragonflies all of which were adults. A vegetarian duck but takes also a few snails, crustaceans and insects. This again is a large duck very similar to the redhead and eats a few such animals as amphibians, fishes, leeches, and mollusks. As the canvasback and the redhead tend to feed along the Altantic coast in brackish water

they come into contact with few dragonflies. When in fresh-water they feed largely on eel grass which grows in deep water where odonate larvae are probably scarce as they are constantly exposed to fish. Thus these ducks come into contact with few dragonflies even when feeding in inland waters.

American Scaup Duck, Greater Scaup Duck, *Nyroca marila* (L.): 752 stomachs examined, 10 with dragonflies, 8 of which were larvae. According to Bent in its summer home in fresh-water (the Arctic Coasts) it lives on small fishes, amphibians, mollusks, insects, and some vegetable food while in its winter habitat on the southern sea coasts it uses less animal food and more vegetable food. Within the coastal waters of the states it is essentially a salt-water and brackish-water duck.

Lesser Scaup, Blue-bill Duck, *Nyroca affinis* (Eyton): 1155 stomachs examined, 176 containing dragonflies. The records show that about 150 of the stomachs contained adults. This is a very active duck which winters during a long season that overlaps late fall and early spring dragonfly flight. This accounts for the greater proportion of adult dragonflies taken. It is also a smaller duck than the two preceding of the same genus, *N. marila* and *N. affinis*. It frequents fresh-water estuaries, sounds and inland waters where it comes into the dragonfly habitat. Because of its smaller size than that of the preceding it eats smaller animals such as insects and fewer mollusks and crustaceans (Cottam 1933).

American Golden-eye Duck, *Glaucionetta clangula americana* (Bonaparte): 175 stomachs examined, 6 with dragonflies, 3 of which were adults. The Survey records indicate that its food is largely crustaceans, mollusks, and insects with vegetable food in moderate amounts. Its short, strong bill would seem adapted to an animal diet. These ducks usually occur on large lakes and rivers where they dive for food. This takes them into deeper water than that in which dragonflies are usually found. Munro (1940) gives Odonata as 2.75% to 11% of the food of the Golden-eye. This rates it as one of the bad bird enemies.

Bufflehead Duck, Butter-ball, *Charitonetta albeola* (L.): 60 stomachs examined, 11 with dragonflies of which 9 were adults. This duck feeds mostly on animal matter, using vegetable matter sparingly. It feeds as does the Golden-eye in the more open fresh waters but from the limited data it takes a larger percentage of dragonflies than do any of the diving sea ducks. This may be associated with its small size as it is only 14-15 inches long, being one of the smaller of the group of sea ducks. Because of its smaller size it probably feeds closer to emergent vegetation in shallower water. In fact, Vernon Bailey states that it is even found at times in small creeks and ponds (Munro 1940).

(The Old Squaw, *Clangula hyemalis* (L.) is a deep water duck taken in Lake Michigan in nets 150 feet deep (Barrows 1912). The three species of Scoters *Melanitta* spp. and *Oidemia*, three species of Eiders *Somateria* and the Harlequin Duck *Histrionicus histrionicus* (L.) are salt water ducks that have no records against them of having eaten Odonata. They frequent open salt water out of the dragonfly environment. They are occasional on the Great Lakes. See Dewar (1915) on diving of British birds.)

Ruddy Duck, *Erismatura jamaicensis rubida* (Wilson): 55 stomachs examined, 4 with dragonflies. It is one of the smaller sea ducks, 13.5-16 inches long, but is most abundant in the marshes and brackish ponds of the western states. It falls in the group of about ten species of scoters, eiders and relatives which are true salt water ducks and seldom, if ever, eat Odonata. It is the smallest of the group and sticks to shallower inland waters which brings it into the dragonfly habitat. It is so small that gunners count four to make a pair in estimating bags. Cottam (1939) found most dragonfly nymphs (3.5% of food) in December.

The Mergansers or Fish Ducks: The mergansers have slender, toothed bills. They eat fish and other small active aquatic animals. The first, the hooded, frequents small shallow streams while the other two are frequenters of more open and deeper waters. As might be expected, the hooded merganser in shallow dragonfly water uses more dragonflies than do the others in deeper waters (Bent 1923; Forbush 1925; Henderson 1927).

Hooded Merganser, *Lophodytes cucullatus* (L.): 50 stomachs examined, 18 with dragonflies, of these 8 were adults and 10 anisopterous nymphs. This species is a frequenter of small streams where it breeds as far south as Tennessee and even Florida, hence it comes more often into contact with adult dragonflies than do the preceding mergansers of more open waters. The food of the hooded merganser is largely aquatic insects with an occasional aquatic animal of other type.

American Merganser or Sheldrake, *Mergus merganser americanus* Cassin: 140 stomachs examined, 2 with adult aeshnids and one with an anisopterous nymph. This species is a fish eater and frequents open waters away from the denser populations of Odonata (Munro & Clemens 1932.)

Red-breasted Merganser, *Mergus serrator* L.: 175 stomachs examined, 6 with adult dragonflies and 4 with nymphs. This species also frequents open waters and is chiefly a fish eater though it includes crustaceans and aquatic insects.

The ducks, aquatic in habit, eat many nymphs as well as some adult dragonflies. The following series of birds, the Order Falconiformes, the hawks, kites and falcons with the exception of the red-shouldered hawk use only adult or flying dragonflies. Thus do kinds of locomotion which limit species to specific habitats effect the nature of the food taken.

The Order Falconiformes contains the most highly developed birds of the Class Aves, *if we think of birds as evolving towards individualism* rather than towards a social life. They are more bird-like in fine vision, ability on the wing and in the more highly

evolved nature of their food (flying insects, birds and mammals). Having evolved in an aerial environment vision has had to have high development as it is the prime distance sense. Birds in general appear to be eye-minded rather than odor- or nose-minded as are the mammals which are associated more closely with the ground and its protective dark holes, warrens and caves where odors have high value. Odor-mindedness is of value in the close contacts of the ground nest or cave, usually dark, where vision is at a discount. Odor-mindedness leads to social life with its numerous close contacts in illy lighted nests and caves. Thus the eye-minded birds of essentially aerial life tend towards individualism. This is in spite of the fact of the high development of the "family" in all higher vertebrates and particularly in the birds. The family behavior is the link between individualism and social life. Thus with this definite trend of bird evolution towards eye-mindedness and individualism the Falconiformes can be rated as structurally our most highly evolved birds in the non-social branch of bird evolution. The swallows and swifts combine fine flight, fine sight and social habits, but have the smaller size that follows social life. Termites are smaller than their ancestral roaches; ants are smaller than their ancestral digger wasps.

This evolutionary trend shows in the extraordinarily acute vision of hawks. They have a high development of both nasal and temporal foveae which gives them both acute monocular and acute binocular vision (Casey Wood 1917). Flight is developed until some, the kites, even mate on the wing and various forms, eagles, vultures, kites, remain on the wing for long hours in their daily flights. Without reduction of speed on the wing they are larger in size than the average bird which makes for greater individualistic abilities. The feet have evolved into raptorial organs which gives the eyes freer use while taking prey. Vision is no longer tied closely to the grasping bill.

Thus in this order we find forms that can match Odonata in speed and ability on the wing. The only factors which keep many of the Falconiformes from using more Odonata are the large size of the bird and the special tastes in some such as the ospreys and vultures. Apparently birds of this order which do eat Odonata take only adults of large species, mainly Aeshnidae which are frequently high, wide fliers. An exception as cited previously is the red-shouldered hawk which fishes at times and captures some odonate nymphs. See also the everglade kite, a mollusk eater (Fisher 1893; May 1935).

FAMILY ACCIPITRIIDAE (hawks, eagles, kites)

This family includes the largest of the raptorial birds. A review of the records following will show that only a few of the smaller species take dragonflies and only occasionally, one might say accidentally. Except the red-shouldered hawk which fishes at times and may take an occasional nymph, the Accipitriidae take only adult dragonflies. Compare the records of this family of the larger hawks with the next family of smaller hawks, the Falconidae, or falcons, where various species appear to catch adult dragonflies regularly.

Certain species and groups of species are out of the dragonfly habitat being upland birds, others are out by size and others by taste. The Harris hawk (*Parabuteo unicinctus harrisi* (Audubon)) of the mesquite regions of the southwest has no records of having taken Odonata. It lives in the dry uplands. The American rough-legged hawk (*Buteo lagopus johannis* (Gmelin)) and the ferruginous rough-legged hawk (*Buteo regalis* (Gray)) are out. The first is a feeder on mammals, the second a bird of the prairie. Three or four other semi-tropical hawks come into the southwest but the food of these has been little studied.

The gray sea eagle (*Haliaeetus albicilla* (L.)) of Greenland eats fish; while the bald eagle (*Haliaeetus leucocephalus* (L.)) eats fish, birds, and mammals; and the golden eagle (*Aquila chrysaetos canadensis* (L.)) confines its food to birds and mammals. The eagles are out of the dragonfly complex because of their greater size.

The ospreys (Pandioninae) eat fish (when not robbed of a meal by some eagle) and are out of the dragonfly environment by both size and taste.

The vultures (Cathartae) eat carrion and do not feed on material as small as insects. They are out of the dragonfly habitat both because of size and taste. (Bent 1937; Fisher 1893; Forbush 1927; Henderson 1927; May 1935; Sutton 1928).

Mississippi Kite, *Ictinia mississippiensis* (Wilson): 15 stomachs examined, one with an adult dragonfly. This species lives largely on flying insects.

(The other kites, swallow-tailed (*Elanoides forficatus forficatus* (L.), white-tailed (*Elanus leucurus majusculus* Bangs and Penard), and everglade (*Rostrahmus sociabilis plumbeus* Ridgway) have no records of stomachs containing dragonflies. The swallow-tailed eats snakes and frogs; the white-tailed a wide mixture of reptiles, frogs, mice and insects; the everglade many large snails, but the Mississippi kite lives largely on flying insects.)

Sharp-shinned Hawk, *Accipiter velox velox* (Wilson): 925 stomachs examined, 2 with adult dragonflies. This hawk lives largely on small birds and mice. Large insects are rarely taken though one of the stomachs listed contained 6 dragonflies. See the pigeon hawk, a falcon.

Cooper's Hawk, *Accipiter cooperi* (Bonaparte): 215 stomachs examined, 2 with adult dragonflies. This, again, preys on birds. In the Yakima Valley (Sunnyside, Wash., 1910-1914) the writer observed it many times on the wing in orchards chasing small birds at full speed under and between closely placed apple trees. Its quick turning ability at full speed on the wing is phenomenal (Johnson 1925). Only occasionally it takes mammals, reptiles, amphibians or insects (Sutton 1928).

(The related species, the Goshawk (*Astur atricapillus* (Wilson)) is a larger bird attacking poultry, game birds, and mammals and rarely takes an insect.)

Red-tailed Hawk, *Buteo borealis* (Gmelin): 510

stomachs examined, one with an adult dragonfly. This Buteo feeds largely on small mammals, reptiles, amphibians, and occasionally on insects and birds (May 1935; Snyder 1936; Sutton 1928).

Red-shouldered Hawk, *Buteo lineatus* (Gmelin): 325 stomachs examined, 6 with adult dragonflies. Three of the stomachs contained the large *Anax junius* (Drury), while one contained 3 nymphs. This hawk feeds on mice, 25%, poultry 2%, crayfish, small fish, and many large insects. Its taste for large insects *and* aquatic animals explains the catch of nymphs (May 1935).

Broad-winged Hawk, *Buteo platypterus* (Vieillot): 90 stomachs examined, one contained an adult dragonfly. This is the smallest of the Buteos and takes few birds and mammals but lives largely on flying insects, caterpillars, spiders, snakes, toads, and crayfish. It would be expected to take dragonflies oftener but it is a shorter winged and more sluggish species that feeds much on the ground (May 1935).

Swainson's Hawk, *Buteo swainsoni* Bonaparte: 30 stomachs examined, one with 2 adult dragonflies. This western Buteo has a diet similar to that of the preceding but takes fewer water animals as it is distributed over the dryer half of North America from Alaska to northern Mexico. Swainson's Hawk uses many grasshoppers in summer and fall (May 1935; McAtee 1935).

(Sennett's White-tailed Hawk, *Buteo albicaudata hypospodius* Gurney: 4 stomachs, one with 1 frog, 1 snake, contained Odonata nymph remains and aquatic insects "considered to be the food of the two vertebrates," Cottam & Knappen 1939.)

Marsh Hawk, *Circus hudsonius* (L.): 530 stomachs examined, 7 with adult dragonflies, one was an Anax. Another stomach contained two. The marsh hawk lives largely on small mammals but takes also frogs, lizards, snakes, insects, and small birds. As its name implies it lives in a dragonfly environment (Coale 1925; May, 1935).

FAMILY FALCONIDAE (falcons, caracaras)

The falcons, of which there are about ten species north of Mexico, are so skilled on the wing that the majority feed principally on birds, this being especially true of the larger forms. One, the sparrow hawk, feeds on Orthoptera, one, the Caracara (*Polyborus cheriway auduboni* Cassin), of the southwest, feeds on carrion, mice, rabbits, snakes, and fish. The three listed as taking Odonata are among the smaller species. Thus, as with the preceding family of hawks, the smaller species are the dragonfly eaters. (Lit. listed by Bent 1938; Forbush 1927; Henderson 1927; May 1935).

Aplomado Falcon, *Falco fusco-coerulescens septentrionalis* Todd; 3 stomachs examined, one with two adult dragonflies. This is a desert hawk of the southwest.

Pigeon Hawk, *Falco columbarius* L.: 700 stomachs examined, 421 with adult dragonflies, 102 containing one dragonfly each and the remainder (319) containing from 2 to 34 each. All of the species of dragonflies that were identified were Aeshninae, including *Aeshna canadensis*, Walker, *A. multicolor*, Hagen; *A. verticallis*, Hagen; *Anax junius*, (Drury); and *Epiaeachna heros* (Fabr.). 120 stomachs contained *Anax junius* the one all-season species. This falcon lives on birds, small mammals and insects. Obviously it takes large dragonflies in large numbers. The above records show 1,872 individual aeshnine dragonflies eaten by 421 pigeon hawks, an average of 4.5 each for the birds whose stomachs contained dragonflies of an average of more than two each (2.67) the average for all stomachs examined. As some of the records represent merely the indigestible chitinous jaws, legs, etc., which may have remained in the bird's stomach for a longer time than that necessary to digest the other parts, these records may represent more than one meal each, or even more than one day's feeding.

Further, a large series of these stomachs came from a hunting preserve on Fisher's Island near New York City where there had been complaint of the large number of pigeon hawks. The majority of the stomachs collected at this place were taken in the late summer and fall after the hawks had migrated along the coast from farther north. (McAtee, W. L., statement to the author.) At that season the fresher coastal marshes swarm with large aeshnine dragonflies. This is the region where they are so abundant that they frequently collect in large so-called "migrating swarms" of dragonflies. Evidently the pigeon hawks on their southward migration came into such a region supercharged with large dragonflies. (Osburn, R. C. 1916; Kennedy 1917, p. 622.) Thus the Fisher Island records probably have a large element of biological accident (Heape 1931).

Before proceeding with a further discussion, it might be well to admit that only about half of the dragonfly remains in this series of stomachs were examined critically but that all so examined contained aeshnine dragonflies.

The fact that no libelluline dragonflies were present is probably not that the hawks avoided them but the fact that the aeshnine dragonflies fly high and wide where they are easily taken by an active hawk while the libelluline dragonflies hug the surface of the water or seldom rise above the marsh vegetation where the hawks would be less liable to take them. Also in the late summer the libelluline dragonflies of the larger species comparable with aeshnines are fewer in number while the aeshnines are at the height of their season. Apparently these bird-eating hawks reacted to dragonflies with a wing spread equalling that of small birds and flying in the same air level.

The record of *Aeshna multicolor*, if correctly determined, came from the stomach of a western specimen as this hawk is distributed from coast to coast with three western subspecies.

Sparrow Hawk, *Falco sparverius* L.: 550 stomachs examined, 32 of which contained remains of adult dragonflies. Eighteen stomachs contained one each, the others two to six each. This falcon lives mainly

on grasshoppers and crickets and thus might be expected to take stray dragonflies. As a rule the sparrow hawk and its western forms are usually found in the open uplands away from dragonfly territory. The southern form (*Falco sparverius paulus* (Home & King)) of the Gulf Coast and Florida may be more closely associated with marshes and such odonate environment. (Breckenridge & Errington 1938.)

This brings us to the Order Galliformes, the "chicken-like" birds which in our area includes the guans (subtropical), grouse, quails, pheasants, and turkeys. As stated below, knowing the insect-eating proclivities of chickens and turkeys, we were surprised that the lowland species, turkeys, quails, etc., did not show dragonflies in their food more often. As a group these birds consume quantities of seeds and insects of the Orders Orthoptera and Coleoptera. On examining their records as reviewed by Henderson (1927, pp. 179-185) we see that they take rather slow insects. On further thought the Galliformes are slow in movement and Casey Wood (1917, pp. 68-70) shows that they have as poorly developed vision as any of our birds. There are no areas of acute vision (foveae) whatever. All have monocular vision. The common hen stares at the visitor with one eye, then turning her head around checks her first impression by staring with the other eye. This is a time-consuming process which would permit fast-moving insects to vacate the premises before any direct action would be forthcoming from the bird. The Galliformes feed while on the ground, are short-necked and usually occupy dry upland.

There are no records of dragonflies being taken by quails (Perdicidae) by grouse, partridges or ptarmigan (Tetraeonidae) or by pheasants (Phasianidae).

FAMILY MELEAGRIDIDAE (turkeys)

The following records, showing few or no Odonata taken by birds of the Order Galliformes was one of the puzzles in the investigation. Having raised turkeys we realized the absolute necessity of animal food in their diet. Wood-swamps are a usual habitat for turkeys from Arkansas to Florida. Perhaps turkeys are not hunted for study much during the dragonfly season when mosquitoes, deerflies, and horseflies are also prevalent. These were the last areas in the United States explored for Odonata and partly on account of biting insects. We would have supposed that quails collected in swamps during the dragonfly season would have left records but quails are usually on the drier ridges. (Bent 1932; Forbush 1927; Henderson 1927; Kozicky 1942).

Wild Turkey, *Meleagris gallopavo silvestris* Vieillot: 19 stomachs examined, 1 with two adult libellulid dragonflies. This is the only Biographical Survey record (up to 1925) of a dragonfly being taken by a gallinaceous bird. It is possible that turkey stomachs collected in the swamps of the southern states might show more Odonata. However, there, insect food is so abundant that the swift dragonflies may be passed for insects more easily taken. (See Kozincky 1942).

The next order, the Order Gruiformes, or "crane-like" birds are not well represented by stomachs in the Biological Survey collection. This may account partly for the few records of their having eaten dragonflies as shown in the Survey's notes. The smaller species, the rails, gallinules and coots live exactly in the areas of densest dragonfly population. All eat a very mixed diet of vegetable matter and small animals. Wood (1917, pp. 71-73) shows that these birds have a fairly acute monocular vision. A distinct nasal (monocular) fovea is present and the area of acute vision is extended by a specialized, narrow band which extends across the retina (Wood, Fig. 120, the coot). The larger species, the cranes, tend to use a more upland environment.

FAMILY GRUIDAE (cranes)

Sandhill Crane, *Grus canadensis tabida* (Peters): 16 stomachs examined, 2 of which contained odonate nymphs, one stomach containing two. This crane eats a wide variety of foods including starchy vegetable products such as bulbs, roots, berries, and grains along with its animal food of reptiles, mice, frogs, toads, millipedes, insects, and molluscs. It is not confined to marsh foods. (Bent, Marsh Birds 1927; Forbush 1925; Henderson 1927).

FAMILY RALLIDAE (rails gallinules and coots)

It is a curious fact that no stomach of rails or gallinules contained dragonflies, either nymphs or adults. As a group they use a very mixed diet of vegetable and animal matter, the latter being mostly invertebrates, such as crustaceans, worms, and molluscs—all slower animals than insects. These birds occupy the same general habitat as the herons but miss the Odonata. However, they are much more secretive in habit and live oftener in the denser portions of the marsh vegetation where dragonflies occur less often. Professor D. J. Borror, while teaching nature study in a boy's camp some years ago, reports having watched a King Rail (*Rallus elegans elegans* Audubon) eat an adult dragonfly. Birds of this family have shorter necks than do the herons and may on this account be less able to take swiftly flying insects. Further, they have a broad taste for vegetable food and the work of Wood (1917) shows in general that vegetable feeders do not have as acute vision as do those birds that feed exclusively on moving animals. (Bent 1927, Marsh Birds; Forbush 1925; Henderson 1927).

Coot, *Fulica americana americana* Gmelin: 40 stomachs examined, 3 containing dragonfly nymphs. The coot is again mainly a vegetable feeder but takes slowly moving animals such as tadpoles, molluscs, crustaceans, etc.

Under the shore birds (Order Charadriiformes) we find two series of families. In the recent A.O.U. Check List the gulls, terns, auks, and murres have been united with the usual shore birds, the plovers, snipe, sandpipers and their close relatives.

The first family, Jacanidae is represented in our area by one Mexican species of Jacana on the Rio

Grande, with no records against it. We find next the aberrant oyster-catchers (Haematopodidae) which have chisel-shaped bills with which they pry open molluscs. These, because of taste for molluscs and the specialized bill, are out of contact with dragonflies. Further, they are usually found on salt water shores. The next series of families are the shore birds proper, the snipe, plover, sandpipers, avocet, stilts, and phalaropes.

As will be seen in the records to follow, the birds of this series live more or less in the dragonfly environment (along shores) but take surprisingly few Odonata. Wood's (1917, p. 79-80) studies show that these birds with a highly developed nasal fovea probably have fairly acute monocular vision. However, many are waders on the water line of the beach, in the edges of the breaking ripples where Odonata, either nymphs or imagoes are seldom found. Dragonflies as nymphs are in slightly deeper water (six inches to six feet) or as adults they fly over deeper water or over the adjacent land or marsh vegetation.

The nymphs, except when crawling out to emerge, avoid breaking waves. The flying adults distribute themselves on the wing according to three interests, that of food (both sexes), that of oviposition (females) and that of sexual desire (males). The food of dragonflies is mainly small Diptera. These usually avoid the wave line and fly over either the emergent vegetation of slightly deeper water or over the vegetation of adjacent low land. Thus dragonflies when feeding tend to be in one or the other place. In oviposition the female odonate usually washes the eggs off the tip of her abdomen (Gomphidae and Libellulidae) in water deep enough for the nymphs or inserts eggs (Zygoptera and Aeshnidae) in emergent vegetation which is usually in water deep enough for the larvae. The males in lust seek the females while ovipositing or while hunting food either of which type of flight tends to take them away from the wave line which is frequented by the smaller snipe, sandpipers, phalaropes, etc. We will connect this banded distinction of dragonflies with the records of the various species that do take Odonata as we come to the species of shore birds which appear to show such.

FAMILY CHARADRIIDAE (plovers)

Of the ten species of plovers listed from our area only four have records of having eaten dragonflies. The plovers are eaters of insects but tend to eat the slower types. They tend to be tide flat or upland birds rather than waders as are the snipe and sandpipers. (Bent 1929; Forbush 1925; Henderson 1927).

Killdeer, *Oxyechus vociferus vociferus* (L.): 260 stomachs examined, 10 with dragonflies, 5 of which were adults. The food of the killdeer is 97% animal matter, mostly worms and insects but as with the other plovers and the snipe, the insects are such things as cutworms, ground bettles, weevils, grasshoppers and other slowly moving forms. This plover feeds on wet flats and sand bars as well as on high dry pastures where it more often nests.

Antillean Killdeer, *Oxyechus vociferus rubidus* Riley: 20 stomachs from Puerto Rico, animal food 98.34%; Orthoptera 16.46%; Coleoptera 32.26%; fly larvae 19.53%; ants 3.92%; snails 19.02%; dragonflies 3.92% (Wetmore 1916).

Golden Plover, *Pluvialis dominica dominica* (Müller): 100 stomachs examined, 4 with dragonflies, all of which were nymphs. This is a bird of the barren grounds in the June breeding season and is the plover that makes the remarkable migratory flights from Nova Scotia across the Atlantic to the pampas of southern South America.

Black-bellied Plover, *Squatarola squatarola* (L.): 440 stomachs examined, 15 with dragonflies, 4 stomachs containing adults. One of these contained 41 Enallagma (Zygoptera) adults. One stomach had 6 nymphs, another 10. This plover is a bird of tide flats only rarely being found inland on fresh water. It breeds on the arctic tundra but spends the late summer on seashore flats. Thus only rarely would it come into the dragonfly habitat. It eats molluscs, worms, crabs, cutworms, grasshoppers, and other insects, also berries.

(Here we will call attention to a relative of the plovers which has taken more positively to the seashore during the winter when and where dragonflies are not present. This is the Surf-Bird (Subfamily Aphrizinae) the stomachs of which might show some Odonata if taken in their nesting grounds in the interior of mountainous southern Alaska.)

The Subfamily Arenariinae, represented in America by two species of Turnstones (Arenaria), has one record of Odonata as food (Knappen 1933, p. 452). Here, again, a relative of the plovers has become a sea-beach bird as a winter visitant. We do not know its food on its arctic breeding grounds. In the winter when Odonata are not on the wing these feed on shore animals, crustaceans, molluscs, etc., along the Atlantic and Pacific Coasts, and as recorded by Knappen eat the bodies of large Odonata (Epiaeshna) washed up on beaches. This is one of the earliest (May) spring dragonflies.

FAMILY SCOLOPACIDAE (snipes, sandpipers, woodcocks, curlews)

(Compare with remarks under the preceding family, the Charadriidae.)

Out of about thirty forms of Scolopacidae found in our area only sixteen have been found to eat Odonata yet the group as a whole, excepting the bartramian sandpiper with upland habits, live almost constantly in a densely populated dragonfly habitat. All eat much animal food of small size and all come within the limits of size for birds that eat Odonata regularly. In the first place the records for many species are incomplete and may show more when more stomachs have been examined. Secondly, many species feed actively and completely exposed at the edge of the water where fewer dragonflies occur than

farther out in the water (nymphs) or farther back in the shore vegetation (adults). (Remarks under Charadriidae.) Their activity and complete exposure while feeding would tend to frighten away adult dragonflies and they would not catch nymphs except when these were crawling out to emerge. Third, they are not exclusively carnivorous but take considerable vegetable food. Wood's work (1917) on the eyes of birds shows that vegetable feeders have poorer eyesight than do strictly insectivorous and raptorial birds and that the retina of the birds of this and the plover families are not adapted for as acute vision as is found in many other birds that catch moving insects or other fast animals. However, in the two examples figured by Wood (1917) (Figure 114, greater yellow-legs and Figure 125, hudsonian curlew) there is an extended and well developed nasal fovea for good monocular vision.

The curious exceptions are the jack snipe and the two species of yellow-legs with perhaps the instance of the solitary sandpiper. Their eyes should be examined to see if they may not have the fovea better developed than is the case in their relatives. (Bent 1927 and 1929; Forbush 1925; Henderson 1927; Spawn 1942).

American Woodcock, ***Philohela minor*** (Gmelin): 130 stomachs examined, 1 with an adult dragonfly. The woodcock feeds largely by probing in soft ground for earthworms and burrowing larvae but stomach records show that it feeds also on aquatic and marsh insects such as click beetles, ground beetles, crickets, ants, etc. It takes also the seeds of marsh plants.

Wilson's Snipe, Jack Snipe, ***Capella delicata*** (Ord): 725 stomachs examined, 139 with dragonflies, 128 of which were nymphs. Apparently this species seldom takes adult Odonata. It feeds quite generally without probing. It takes seeds of marsh plants, snails, worms and many of the slower aquatic and marsh insects of considerable size.

Eskimo Curlew, ***Phaeopus borealis*** (Forster): 4 stomachs examined, 1 containing an adult dragonfly. This is a marsh and upland bird with plover habits. It is on the verge of extinction, (the last one seen, April 8, 1926, as reported in the A. O. U. List, 1931) but was an inhabitant of the Barren Grounds and a transient in the United States. (Cottam & Knappen 1939).

The curlews, the long-billed and hudsonian, are shore birds living on a very mixed diet of seeds, berries, crustaceans, molluscs, worms, spiders, and insects. All three species have long down-curving bills which may hinder them in catching active insects as is shown by the foods listed above. Thus the curlews are a group living in a dragonfly habitat but catching few of these.

Bartramian Sandpiper, Upland Plover, ***Bartramia longicauda*** (Bechstein): 200 stomachs examined, 1 of which contained an adult dragonfly. It is a sandpiper-like bird which lives in the uplands with plover habits. It feeds on grasshoppers, locusts, crickets, white grubs, and cutworms, slow insects.

Solitary Sandpiper, *Tringa solitaria* Wilson: 7 stomachs examined, 1 containing 2 nymphs. Wetmore (1916) reports two stomachs of birds taken in Puerto Rico the contents of which were nearly one-half dragonfly nymphs. A bird of woods pools, Barrows (1912). This remarkable bird needs study. It nests in woodland birds' abandoned nests. It catches insects on the wing and can stand on one leg while it stirs up aquatic insects waving its free foot in the water. With only 7 records the number of nymphs is startling. (Forbush & May 1939).

Willet, *Catoptrophorus semipalmatus* (Gmelin): 230 stomachs examined, 16 with dragonflies of which 6 contained adults, 1 with 3 and 1 with 14. Of the stomachs with nymphs 2 had 2 each, one 14 and one 18. This is a shore bird of sandpiper habits eating crustaceans, molluscs, marsh and aquatic insects, and a few small fish. As it is a bird of sea beaches as well as of fresh waters those collected on sea beaches would have had few Odonata. (Forbush & May 1939).

Greater Yellow-legs, *Totanus melanoleucus* (Gmelin): 702 stomachs examined, 153 with Odonata, only 27 of which were adults, mostly 1 each, but 1 stomach contained 39 and another 31 adults, while many stomachs (37) contained from 4 to 110 nymphs each. Eight stomachs had each over 30 nymphs. This bird is a giant sandpiper and its food contains amphipods, top minnows, swimming insects, and worms. See the next for comment. (Allen, G. M. 1925; Danforth 1926).

Lesser Yellow-legs, *Totanus flavipes* (Gmelin): 760 stomachs examined, 123 with dragonflies, 43 of which were adults. Four stomachs had 2 and two had 3 adults each. Sixteen stomachs had 2 nymphs each, five had 3 each, five 4 each, five 5 each, five 6 each, one 8, one 10, two 11, one 12, one 14, one 15, one 18, one 26, one 60 and one 120 nymphs, the last item all Zygoptera. Twenty-seven of the stomachs contained anisopterous nymphs. This species again has sandpiper habits and eats many fish and aquatic insects.

The two species of yellow-legs are surprises in the large number of dragonflies eaten by them. These are mostly nymphs with large numbers in many of the stomachs. Of adults the lesser yellow-legs appears to take more than twice as many as the greater. Roughly about 20% of the food of each species consists of dragonflies. Obviously they are in a different class from that of the other sandpipers. Their greater size may account for this. The sandpipers feed at the edge of the water where there are few dragonflies except when these emerge. Dragonflies seldom occur in the top six inches of the water and seldom fly in the six inches just above the water. The greater height of the yellow-legs may permit them to reach farther up in the air and deeper into the water. The greater number of adults taken by the lesser may indicate distinct food preferences. Doctor Edward S. Thomas, Curator of Natural History in the Ohio Archaeological Museum, an experienced student of birds, stated to the author that the

lesser is more active than the greater. (See Forbush & May 1939 for habits; Bent 1927; Allen, G. M. 1925; Howell 1924).

Knot, *Calidris canutus rufus* (Wilson): 215 stomachs examined, 2 with adult Anisoptera. With the Knot we come into a group of snipe and sandpipers with shorter and heavier bills, that apparently take adult dragonflies as easily as nymphs. The preceding long-billed species caught more nymphs than adults.

Pectorial Sandpiper, *Pisobia melanotos* (Vieillot): 104 stomachs examined, 3 stomachs with Odonata, each of which contained 3 adults. Food, various insects, worms, molluscs, and plants.

Baird's Sandpiper, *Pisobia bairdi* (Coues): 45 stomachs examined, 7 contained Odonata, only one stomach containing a nymph, while another contained 5 adults. Food consisting of seeds of marsh plants mixed with marsh insects.

Dowitcher, Red-breasted Snipe, *Limnodromus griseus griseus* (Gmelin): 200 stomachs examined, 89 with Odonata, 4 of which were adults and one stomach contained 3 adults. Two stomachs contained 3 nymphs each and one had 2. The dowitcher takes more aquatic plant seeds than usual among snipes and besides insects takes molluscs, small fishes, and crustaceans (Spawn 1942).

Long-billed Dowitcher, *Limnodromus griseus scolopaceus* (Say): 90 stomachs examined, 6 with dragonfly larvae. The general food of this species is similar to that of the dowitcher.

Stilt Sandpiper, *Micropalama himantopus* (Bonaparte): 15 stomachs examined, 3 with odonate nymphs. Its food contained many aquatic insects.

Marbled Godwit, *Limosa fedoa* (L.): 90 stomachs examined, 1 with an adult dragonfly. Food more aquatic than the preceding, crustaceans, aquatic insects, worms, leeches, snails, and some vegetable food.

FAMILY RECURVIROSTRIDAE (avocets and stilts)

These rather large, slender, snipe-like birds have long needlelike bills which in the avocets curve up very decidedly, less so in the stilts. In spite of the peculiar bill they catch many aquatic insects, including dragonfly nymphs and even small fish. In walking and wading with their long stilt-like legs they appear slow and awkward but in the use of sight and in the use of neck and bill they appear from food records to be able to take active prey swimming in or on the surface of the water. (Bent 1927; Forbush 1925; Henderson 1927; Wetmore 1925).

American Avocet, *Recurvitostra americana* (Gmelin): 55 stomachs examined, 3 containing dragonfly nymphs, one stomach with 3 nymphs. The American Avocet is a bird of the shores of inland waters where it feeds by moving its long, needle-shaped bill about over the bottom so that it finds much of its food by the sense of touch. This habit of feeding accounts for nymphs.

Black-necked Stilt, *Himantopus mexicanus* (Müller): 70 stomachs examined, 9 with dragonfly nymphs, one stomach containing 3. The food of this species includes crayfish, Coricidae, caddisfly larvae, small fish and some land insects such as grasshoppers. As observed by the writer on the marshes of the Yakima Valley, Wash., it is a slow, awkward bird and may be too slow to take adult Odonata easily. Another factor may enter but one on which we took no observations. On the mud shores a black-necked stilt is so tall and conspicuous adult dragonflies may recognize any slight movement and avoid capture. Among other shore birds this stilt is startlingly conspicuous to the human observer.

FAMILY PHALAROPODIDAE (phalaropes)

This is a family of curious birds intermediate in leg and foot structure between the rails and the snipes. They look like snipes, some have lobed feet like rails and they swim like ducks. (Personal observations on Wilson's phalarope in the Baker Valley, Ore., marshes.) The female is more brightly colored than the male and the latter broods the eggs. They swim and wade in shallow open waters.

This is another family of birds of the general size that eat Odonata. They live in the midst of a dragonfly environment (except the red phalarope in winter) and feed on an animal diet including insects. Why do they not use more dragonflies? The odd red phalarope is pelagic in our area, being found off the coast in winter and apparently does not come to land except in storms. Its food is mainly crustaceans. (Bent 1927; Forbush 1925; Henderson 1927; Wetmore 1925).

Wilson's Phalarope, *Steganopus tricolor* Vieillot: 105 stomachs examined, one with a dragonfly larva. This phalarope feeds on aquatic and terrestrial insects, snails, etc.

Northern Phalarope, *Lobipes lobatus* (L.): 150 stomachs examined, 3 with adult Odonata. The food of this species consists of aquatic worms, crustacea, insects, with a few seeds of marsh sedges.

FAMILY LARIDAE (gulls and terns)

The gulls in general are scavengers and feeders on small animals both land and marine, including the larger insects such as Orthoptera and Odonata. In this problem too little is known about the food fed to nestlings. The evidence cited in this article is mostly from adult stomachs. See Franklin Gull below where dragonflies (larvae) are fed the young. The terns tend to eat small, live fishes more often than do the gulls, perhaps because of greater agility on the wing. The eyes in this family have good monocular vision, a nasal fovea, but only gull eyes were studied by Wood (1917). The ability of the terns to strike fish from the air as a falcon strikes suggests better vision than that in the scavenger gulls.

The gulls and terns are marine birds usually nesting on the ground or on floating vegetation in marshes. They nest in colonies and have young that mature slowly so that colonies survive only on inviolate nesting sites. Thus the nesting site, the swallow-like ability on the wing and

a taste for large insects set the limits on their use of dragonflies as food. The nesting site appears to be the main limit as the eggs and young have to be protected from ground vermin by water. The scavenger gulls appear to use dragonflies less often than the raptorial terns. (Bent 1921, 1947; Forbush 1925; Henderson 1927.)

Ring-billed Gull, *Larus delewarensis* Ord: 50 stomachs examined of which 4 contained adult Odonata. This species feeds much on insects, small rodents, etc., only 29 of the stomachs containing small fish.

Franklin's Gull, *Larus pipixcan* Wagler: 125 stomachs examined, 8 with remains of dragonflies. McAtee records one stomach with 327 odonate nymphs while Roberts records another stomach taken in the nesting season with 321 nymphs. Judd (1901) quotes Roberts (1900): "The parent birds were feeding their young by regurgitating into them the nymphs of dragonflies." This gull nests on the fresh-water ponds of southern central Canada, the Dakotas, and Minnesota and is almost wholly insectivorous being the most beneficial of the gulls. Its diet is largely insects of some size such as Orthoptera, caterpillars, aquatic bugs, grubs, etc., which it hunts over the dryer fields as well as over marshes. (Beal 1912b).

Common Tern, *Sterna hirundo hirundo* L.: 116 stomachs examined. Food, besides fish, moths 2%, other insects including Odonata, Orthoptera, ants, Coleoptera, etc., 1.5% (McAtee & Beal 1924).

Arctic Tern, *Sterna paradisaea* Brünnich: 45 stomachs examined, 5 containing dragonfly nymphs, 30 contained small fish, 8 had crustaceans but the bulk of the food is marsh and aquatic insects. This species breeds in inland waters as well as on the northern coasts.

Black Tern, *Chilidonias nigra surinamensis* (Gmelin): 280 stomachs examined, 42 contained adult dragonflies. This is the common species in the inland marshes of the northern states. Here it has the flight of a giant swallow and is almost wholly insectivorous. McAtee and Beal (1924) give dragonflies as 20% of its food, mayflies 13%; grasshoppers 12%, and small fishes 19%.

Two other terns nest on fresh-waters in the interior, the Caspian *Hydroprogne caspia imperator* (Coues) and the least tern *Sterna antillarum antillarum* (Lesson). Both are fish eaters. The six or more other species in North America are marine birds.

FAMILY ALCIDAE (guillemots, auks, murres, puffins)

While we have listed the Alcidae among the sea birds that do not eat Odonata one record stands against one species. The group as a whole feed almost entirely on sea fishes and crustaceans. (Bent 1919).

Black Guillemot, *Cepphus grylle grylle* (L.): 15 stomachs examined, 1 with an adult dragonfly. This is a salt-water bird that feeds on small fish, isopods, amphipods, and marine worms. The dragonfly, probably a windblown individual, may have been picked up on a beach while the bird was searching for crustaceans and worms.

(Classed in the Order Charadriiformes with the Laridae are the families Stercorariidae (Jaegers) and Rynchopidae (Skimmers). These are strictly marine birds which do not normally enter a dragonfly habitat in fresh- or brackish-waters. Together with the preceding family, the Alcidae, we have classed these in our first division of birds, those which do not eat Odonata.)

This closes the series of water and shore birds in our fauna, a series which in many ways is primitive as bird evolution goes and which feed largely or wholly on animal matter (exception, the geese). As a whole they are more closely associated with the habitat of the aquatic Odonata, particularly the nymphs of dragonflies than are the next series of Orders, the more strictly land birds.

(There are no records of dragonflies taken by pigeons or doves, Order Columbiformes, all of which are fruit and seed eaters and which we have already classed with the series of families that do not eat Odonata.) (See Chard, 1937).

No records stand against the parrots, Order Psittaciformes, represented at one time by the now extinct Carolina and Louisiana paroquets. Perhaps we could include here the skeletons of the Mexican military macaw found in numbers near Flagstaff, Arizona about pueblo ruins on the Wupatki National Monument. ("Nat. Hist.," 1948, 57: 41.) Parrots in general are vegetarians, largely fruit eaters.

FAMILY CUCULIDAE (cuckoos, anis, road-runners)

The anis and road-runners, Order Cuculiformes, eat an extraordinarily diverse mixture of small animal life but there are no observations or records of their having used dragonflies as food. The road-runners are usually found in very dry habitats where Odonata seldom occur. The anis are lowland birds of pastures and farming areas where they frequently follow cattle as do cow-birds. They occur on the southern edge of our area.

Both northern cuckoos are shy birds that remain much of the time in the foliage of trees though the nest is often low. Dragonflies prefer the surface of lower vegetation-stands and open places. No data has been found on Maynard's cuckoo of the mangrove swamps of the southern tip of Florida. (Beal & Judd 1898; Bent 1940; Forbush 1927; Henderson 1927).

Yellow-billed Cuckoo, *Coccyzus americanus americanus* (L.): 340 stomachs examined, 10 of which contained adult dragonflies, 1 stomach containing 2 and another 8. From the last record we may infer that they catch Odonata, if plentiful and easily taken, but otherwise usually feed on arboreal insects. Both the yellow-billed and black-billed cuckoos are birds of the dense tree tops where dragonflies seldom occur. (Beal, McAtee & Kalmbach 1941).

Black-billed Cuckoo, *Coccyzus erythropthalmus* (Wilson): 160 stomachs examined, 8 of which contained adult dragonflies. Both cuckoos are almost wholly insectivorous. The black-billed cuckoo hunts over low, wet areas more often than does the yellow-

billed (Forbush & May 1939) which is an arboreal bird. The scant data indicates about twice as many dragonflies are eaten by the black-billed.

The next, the Order Strigiformes, contains the owls which in general are nocturnal. However, not all owls are wholly nocturnal and not all Odonata are wholly diurnal. Thus, as far as flight time is concerned, some species from each group can contact species of the other group. The majority of owls are of the order of size of birds that catch Odonata and all are flesh eaters.

FAMILY TYTONIDAE (barn owls)

The Family Tytonidae, or barn owls, of which we have one species *Tyto alba paratincola* (Bonaparte) in our area, apparently never eat dragonflies. A great amount of data has been obtained on the food of this owl by the collection about nests and roosting places of the pellets of indigestible parts that are regurgitated. The student of bird-foods collects and analyzes these. This applies also to the next family, the horned owls. The barn owl lives almost exclusively on small mammals. (See Lantz 1906; Fisher 1896.) It is the most highly specialized of our native owls in that it is the most deeply nocturnal of owls. This latter character puts its activities so far into the night that it must seldom come into contact with even those species of Odonata (Aeshninae spp.) that tend to be crepuscular. Its lack of interest in insects as food in general also separates it from the dragonfly complex. (Bent 1938; Forbush 1927; Henderson 1927.)

FAMILY STRIGIDAE (horned owls)

Of the fifty-six varieties of owls in our region only two have records of having eaten dragonflies. In general dragonflies are very diurnal, flying usually only in direct sunshine. Owls are generally nocturnal though various forms hunt on dark days, in twilight, etc. The records are of the less specialized family, the Strigidae, many of which can hunt in intermediate light. The owls appear to take dragonflies less often than do hawks of the same order of size. The larger owls use mice as a large part of their diet. (Bent 1938; Forbush 1927; Henderson 1927).

Screech Owl, *Otus asio naevius* (Gmelin): 440 stomachs examined, 3 contained adult dragonflies. The screech owl in its ten or so forms uses a great variety of food including small mammals, birds, reptiles, crustaceans, and insects. (Allen, A. A. 1924; Clabaugh 1926; Lantz 1906).

Pigmy Owl, *Glaucidium gnoma* Wagl.: 50 stomachs examined, 1 contained an adult *Aeshna palmata* Hagen. This is a diurnal owl that lives largely on insects but can eat small birds. It is a woods owl and thus misses most of the dragonflies except such as *Aeshna palmata* that frequently flies in beats in open glades of woods bordering on streams. The six subspecies of pigmy owl listed in the A. O. U. Check List are lumped in this instance. (Johnson 1903).

The Order Caprimulgiformes (Goatsuckers) in our area contains 17 named forms, including the chuck-will's widow, whip-poor-wills, one pauraque (lower Rio Grande), and nine subspecies of nighthawks. Only three of the goatsuckers (Caprimulgidae) have dragonflies charged aaginst them.

FAMILY CAPRIMULGIDAE (goatsuckers)

The goatsuckers are nocturnal birds but all will fly on cloudy days. The nighthawk has the habit of flying before and after summer storms, and has the swallow habit of flying over water which may account for the dragonflies in its food. The nighthawk has taken to nesting in cities on high tar-gravel roofs from where it flies widely over wooded suburbs. All records are for adult dragonflies.

The goatsuckers are large flying insect traps. Because of their large size they take larger insects than do the swallows; further, they are crepuscular and nocturnal when more large insects fly to greater heights than do insects generally in daylight hours. The crepuscular nighthawks which fly in the dusk before storms and at twilight take many flying ants, many species of which swarm on sultry evenings.

The food listed against various species suggests that some, at least, feed on the ground. The whip-poor-wills regularly patrol bare knolls in their breeding areas as can be told from their night calls from such areas. In general their contacts with dragonflies are with those normally diurnal species which also tend to fly into the twilight. (Bent 1940; Forbush 1927; Henderson 1927).

Chuck-will's-Widow, *Antrostomus carolinensis* (Gmelin): 40 stomachs examined, 4 contained adult dragonflies, 1 being the very large *Epiaeschna heros* (Fabr.) which frequently flies into the dusk as do several species of Aeshninae. This is the largest of the North American goatsuckers and occasionally eats small birds though usually taking large insects on the wing, such as moths and night-flying beetles. (Beal, McAtee & Kalmbach 1941; Bowdish 1902, 1903).

Nighthawk, *Chordeiles minor minor* (Forster): 315 stomachs examined, 22 containing adult dragonflies. One contained 13 individuals of the rare *Ischnura prognata* Hagen, a zygopter. Fourteen stomachs contained other Zygoptera and 8 contained Anisoptera. (Beal 1903).

Texas Nighthawk, *Chordeiles acutipennis texensis* Lawrence: 20 stomachs examined, 1 contained an adult dragonfly. The food of this species consists of miscellaneous flying insects, especially beetles and moths. (No published records of *texensis*).

The Order Micropodiiformes (the small footed birds) includes the swifts and hummingbirds.

With the possible exception of some hummingbirds such as our very nectarofagous ruby-throated hummingbird, *Archilochus colubris* (L.), both swifts and hummingbirds are insectivorous, the swifts scooping insects during a steady winging flight, the hummingbirds operating from high perches more as do flycatchers. The swifts are of an order of size large

enough to take small dragonflies. The hummingbirds are generally so small that they normally use much smaller insects.

FAMILY MICROPODIDAE (swifts)

Only one swift is abundant enough that a series of stomachs has been collected. Probably all four swifts in our area take small Odonata at times though the black swift *Nephoecetes niger borealis* (Kennerly) and the white-throated swift *Aeronautes saxatalis saxatalis* (Woodhouse) nest and fly at such great elevations that they may seldom contact Odonata. The swifts, again, are flying insect traps but normally use insects smaller than the smallest Odonata. (Bent 1940; Forbush 1927; Henderson 1927).

Chimney Swift, *Chaetura pelagica* (L.): 150 stomachs examined, 7 with adult Odonata, 2 of which were Anisoptera and 5 Zygoptera. This bird is wholly insectivorous and the records show that it sometimes takes insects as large as locusts.

(The Hummingbirds, Family Trochilidae, are largely insectivorous though they feed on nectar in season but are so diminutive that they do not take insects much larger than gnats and minute parasitic Hymenoptera. Apparently the species of this family are below the size necessary to take Odonata easily.) (Bent 1940; Forbush 1927; Henderson 1927; Lucas 1893).

(The American Trogons, Family Trogonidae, Order Trogonoformes, of which one species extends into southern Arizona, live on fruits and insects including large forms such as grasshoppers.) (Henderson 1927, p. 208).

The Order Coraciiformes is largely a tropical group which includes the many kingfishers, motmots, rollers, bee-eaters and hornbills. Only the belted kingfisher interests us.

FAMILY ALCEDINIDAE (kingfishers)

This very specialized family is represented in our area by the eastern and western forms of the belted kingfisher, and casually on the Mexican border by two tropical species. The belted kingfisher is a noisy, frank but interesting land bird which, while it swims little manages to live comfortably off of swimming fish and other moving aquatic animals. (Bent 1940; Bowdish 1902-1903; Forbush 1927; Henderson 1927).

Belted Kingfisher, *Megaceryle alcyon alcyon* (L.): 330 stomachs examined, 33 with dragonfly nymphs, 1 to a stomach except 2 that contained 2 nymphs each. The food of the kingfisher is mainly live fish but it contains also 16% crayfish, 4% batrachians, and 3% insects. It takes only moving, swimming animals. By food habits the kingfisher is a diving water-fowl. (See Part III. Taxonomy of kingfisher.)

The Order Piciformes includes the woodpeckers, toucans, jacamars and barbets, the latter three tropical. This in structure and habits is one of the most highly specialized groups of birds.

FAMILY PICIDAE (woodpeckers)

The 1931 A. O. U. Check List records sixty species and subspecies in our area. Only three forms have Biological Survey records showing the use of dragonflies as food. Woodpeckers live on insects, fruits and seeds but have such highly specialized habits in feeding either on the trunks of trees or on the ground that they seldom encounter Odonata. (Beal 1911; Bent 1939; Forbush 1927; Gardner 1927; Henderson 1927; Lucas 1895).

Northern Flicker, *Colaptes auratus luteus* Bangs: 700 stomachs examined, 2 contained adult dragonflies. This species feeds frequently in open fields on the ground on the larger field species of ants where it could easily pick up wind-blown dragonflies or those strayed away from neighboring streams and slowed down by cool weather. (Knowlton & Stains 1943).

Yellow-bellied Sapsucker, *Sphyrapicus varius varius* (L.): 325 stomachs examined, 2 contained adult dragonflies.

This species cuts rows of holes into the bark of thin-barked trees. It eats the cambium (10% to 20% of stomach contents) brushes out the sweet sap with its short hair-tipped tongue (Lucas 1895), and catches the insects attracted to these traps baited with sap. This damage to valuable trees, mainly orchards, has been estimated at over one million dollars annually. (Beal 1913). This very specialized habit of feeding keeps its attention applied largely to areas free of dragonflies. However, birch trees which usually grow near water are attacked by it. The dragonflies taken were probably chilled and roosting on tree trunks in cool weather. Because of this "sapsucking" habit the yellow-bellied sapsucker has had more than its share of persecution by orchardists and an unusual amount of scientific publicity.

Downy Woodpecker, *Dryobates pubescens medianus* (Swainson): 750 stomachs examined, 1 with an adult dragonfly. In the genus Dryobates the tongue is long and is used in probing insect galleries in tree trunks for wood boring larvae. A dragonfly would be the accidental take of one chilled and resting on a tree trunk. This woodpecker and related innocent species have been carefully checked along with the sapsuckers in Biological Survey studies hence the number of published studies.

THE PASSERIFORMES

With the Order Passeriformes or perching birds we complete this study. Ornithologists place this as the highest and latest order in evolution of bird life. They are fartherest in structure and habits from ancestral dinosaur types. (See remarks under Order Falconiformes on the evolutionary position of the hawks, eagles and falcons, and the remarks on the primitive habits of the kingfisher under Part III.) Apparently birds evolved from aquatic or semi-aquatic dinosaurs that inhabited the sea shore and the Mesozoic lakes and streams. The land birds appear to have arisen in a dragonfly environment and then in later evolution to have evolved out of such an environment onto higher and drier land.

The perching birds in general are land and tree forms. Usually they are highly insectivorous. Some are almost wholly so and nearly all raise their young

on an insect diet, even to those forms that are seed and fruit feeders as adults.

No bird-food study made so far indicates that any species of insectivorous perching bird lives exclusively on any one kind of insect, even any one order of insects. The insectivorous forms take all insects up to the largest usable size, in the case of the larger bird species all sizes down to those too minute for the size of the bird. Thus they eat adult dragonflies, if such stray into higher ground and whenever the bird lives over or near the water. A few stream-bank scavengers get dragonfly nymphs as these crawl from the water to emerge. The insect-egg-eating birds occur in this order, the small twig and tree-trunk searchers such as nuthatches, creepers, titmice, warblers, vireos, etc. Dragonfly eggs are not taken by these egg-eaters because dragonfly eggs are either dropped into the water or are placed with the use of an ovipositor beneath protective surfaces.

FAMILY TYRANNIDAE (tyrant flycatchers)

Seventeen of the thirty-five forms of tyrant flycatchers found north of Mexico are recorded as taking dragonflies occasionally. Only three or four take them with any regularity. This is in spite of the fact that many of the species of this family have the habit of nesting near water and all are very insectivorous. Their food in general shows that they prefer Hymenoptera and Diptera with some of the smaller Coleoptera and Hemipteroidea. Some of the tropical Tyrannidae as told the author by E. B. Williamson, deceased, formerly banker of Bluffton, Indiana, and Col. F. C. Fraser, I.M.S., Bournemouth, England, both experienced dragonfly collectors in tropical lands, are much more specifically dragonfly eaters. (Beal 1912a; Bent 1942; Forbush 1927; Henderson 1927).

Eastern Kingbird, *Tyrannus tyrannus* (L.): 700 stomachs examined, 39 with adult dragonflies. Those identified are the small anisopter, *Leucorrhinia intacta* (Hagen) and the zygopters, *Agrion* sp. and *Argia* sp. Food, 10% fruit, 90% insects, over half of which are Coleoptera and Hymenoptera. In the western United States the kingbird nests in trees along streams and probably there catches more Odonata. Because of the reputation of the kingbird for catching honey bees it has been studied extensively by the Biological Survey. Its other common name is bee bird. The Biological Survey publications up to 1911 on the food of the kingbird are listed by McAtee 1913. (Knappen 1933).

Arkansas Kingbird, *Tyrannus verticalis* Say: 145 stomachs examined, 3 with adult dragonflies. This is a western desert bird nesting in the forks of large trees along streams but since man's arrival it nests on telephone poles, hay derricks, etc., miles from original streams. (Beal 1912).

Cassin's Kingbird, *Tyrannus vociferans* Swainson: 45 stomachs examined, one with an adult dragonfly. (Beal 1910).

Scissor-tailed Flycatcher, *Muscivora forficata* (Gmelin): 130 stomachs examined, one only with an adult dragonfly. This is a bird of the open southwestern prairies and mesquite plains where dragonflies are few in number, Orthoptera constitutes 46% of its food. (Beal, McAtee & Kalmbach 1941).

Northern Crested Flycatcher, *Myiarchus crinitus boreus* Bangs: 265 stomachs examined, 23 with adult Odonata. Mr. E. B. Williamson reported by letter to the writer that this species is one of the worst offenders in its catching of Odonata.

The northern crested flycatcher has a record of one stomach out of ten with dragonflies. But E. B. Williamson, dragonfly specialist, watched a pair with a nest in a hole of a tree on the banks of the Wabash River, three blocks from his home at Bluffton, Indiana. Before they built the nest large Macromia dragonflies were abundant on that stretch of the Wabash. In three or four years the Macromias became rare. The flycatchers caught them persistently. He attributed the scarcity of Macromias to the one pair of northern crested flycatchers. This specialized taste does not show in the Biological Survey records. The crested flycatcher nests widely. As a boy we found a nest with its characteristic snake skin in a hollow black walnut, where probably few Odonata ever occurred one mile from the nearest water.

Collectors of dragonflies in the tropics report species of Tyrannidae that at least individually are persistent catchers of dragonflies. These observations made by experienced field men do not agree with stomach records based on long series of stomachs of any one species. Several cases appear in the records where one stomach is gorged with dragonflies while the others of the same species of bird may have one or a few or more. We believe that individual birds develop a taste for one type of prey and may individually become addicts to that one kind of insect. Wolves and other mammalian carnivora are known to become individual specialists on special prey. We even observe special tastes developed around the breakfast table at home.

Ash-throated Flycatcher, *Myiarchus cinerascens* (Lawrence): 90 stomachs examined, 6 with adult dragonflies. This is a desert bird that frequently breeds several miles away from water.

Eastern Phoebe, *Sayornis phoebe* (Latham): 365 stomachs examined, 11 with adult dragonflies. Three of these contained Zygoptera while 8 contained Anisoptera, one stomach having the remains of 12 of the latter. For an insectivorous bird of its size and with the habit of nesting over water, the Phoebe catches relatively few dragonflies. It is well classed as a fly (Diptera) catcher.

Black Phoebe, *Sayornis nigricans nigricans* (Swainson): 340 stomachs examined, 67 with adult dragonflies. This species uses more mud in the construction of its nest than do the preceding, the nests of which are largely of moss, trash, feathers, etc. As this is a bird of the dry southwest its nest material may indicate that it is more closely associated with streams even than the preceding which may account for the fact that it eats 3-5 times as many dragonflies as either of the others. The stomach contents show

that the Black Phoebe is "one of the most exclusively insectivorous of the family" of tyrant flycatchers.

Say's Phoebe, *Sayornis saya saya* (Bonaparte): 130 stomachs examined, 7 with adult dragonflies. This is a bird of the western plains and mountains but has the same habit as the Eastern Phoebe of nesting near water.

Yellow-bellied Flycatcher, *Empidonax flaviventris* (Baird and Baird): 105 stomachs examined, 2 with adult dragonflies. This is a bird of bogs and woods swamps living in a dragonfly environment but using comparatively few as food.

Alder Flycatcher, *Empidonax trailli trailli* (Audubon): 155 stomachs examined, 9 with adult dragonflies. This is a northern bird nesting near water and is small in size. This is distinctly a stream loving bird but prefers Hymenoptera and other small insects.

Least Flycatcher, *Empidonax minimus* (Baird & Baird): 170 stomachs examined, 4 with adult dragonflies. This is the smallest of the flycatchers of our area except the buff-breasted flycatcher of northwestern Mexico. It is smaller than a chipping sparrow and is one of the smallest birds that eats dragonflies, comparing in size with the smaller swallows, the wrens and the warblers.

Wright's Flycatcher, *Empidonax wrighti* Baird: 20 stomachs examined, one with an adult dragonfly. This is a bird of the Great Basin desert and is usually found near streams. (No published data.)

Western Flycatcher, *Empixonax difficilis difficilis* Baird: 162 stomachs examined, one only with one adult dragonfly. This is a western bird of the small size of the wood pewee and nests near water. Obviously it prefers other insects than Odonata. The records show about 40% Hymenoptera and 30% Diptera.

Eastern Wood Pewee, *Myiochanes virens* (L.): 365 stomachs examined, 14 with adult Odonata, one stomach containing 5. This is a bird of the open glades of the eastern deciduous forest. According to Forbush (1927) the wood pewee has been known to catch small trout from hatchery ponds.

Western Wood Pewee, *Myiochanes richardsoni richardsoni* (Swainson): 165 stomachs examined, 19 with adult dragonflies. Deciduous woods are preferred by flycatchers. In the West these tend to be along streams which may account for the western wood pewee's large take of Odonata.

Olive-sided Flycatcher, *Nuttalornis mesoleucus* (Lichenstein): 60 stomachs examined, 6 with adult dragonflies: a bird of the northern coniferous forest, a tree-top bird when feeding.

(We pass over the larks, Alaudidae, the skylark which has been introduced, and the sixteen subspecies of the native *Otocoris alpestris* (L.) or horned lark. These are birds of high dry areas that nest on the ground and feed on the dry ground. Either habit is seldom associated with catching dragonflies when it is found in other birds. There are no records against them.)

FAMILY HIRUNDINIDAE (swallows, martins)

The swallows have been investigated extensively by the Biological Survey perhaps partly because they are so obviously beneficial in their food habits and thus made good evidence for the protection of the smaller birds, partly perhaps because around barns the barn swallow at times litters well-kept premises with unsightly nests.

Swallows tend to fly over or near water, live on insects exclusively and are large enough to take the smaller dragonflies. However, the evidence from stomach examination suggests that they are on the borderline in size. The smaller swallows do not take dragonflies as regularly as do the larger martins which appear to be among the outstanding eaters of small Odonata. The martin boxes of the country-home are more often regularly successful in attracting nesting pairs where there is a considerable stream or body of water near.

The evidence is that the martins are enemies of dragonflies. Apparently they hunt for them. Perhaps the larger size of the martins as compared with the other swallows gives them an advantage over the smaller swallows in taking insects as large as dragonflies. What the limits are that protect dragonflies by keeping the populations of martins low is difficult to say, but social animals are usually preyed upon heavily by disease, parasites and predators. Further, the highly specialized nesting sites of the martins, while protecting them from predators, limit the population of martins by the scarcity of nesting sites. (Beal 1918; Bent 1942; Forbush 1929; Henderson 1927).

Tree Swallow, *Iridoprocne bicolor* (Vieillot): 330 stomachs examined, 32 with adult Odonata. The tree swallow is most abundant along the Atlantic coast and usually nests near water. Barrows (1912, p. 550) records it catching early spring stoneflies with the temperature 2-3 degrees above freezing.

Bank Swallow, *Riparia riparia riparia* (L.): 415 stomachs examined, 33 with adult dragonflies. This is the sand swallow of Europe with habits identical with those of this American group. From the records, the bank swallow appears to catch Odonata twice as often as does the rough-winged swallow. The bank swallow, before the advent of railroad engineers with their cliff-producing cuts, found its clay-bank nesting sites almost entirely in banks over or near water and it still flies almost entirely over or near water. On the other hand, the rough-winged swallow seldom makes its own holes but nests in any crevice or cranny that is convenient and so probably does not feed as often over water. See notes on the martin.

Rough-winged Swallow, *Stelgidopteryx ruficollis serripennis* (Audubon): 135 stomachs examined, 4 with Odonata. This species nests in vertical banks in any convenient hole.

Barn Swallow, *Hirundo erythrogaster* Boddaert: 467 stomachs examined, 35 with adult dragonflies. As with the cliff swallow this bird has adapted its

nesting to the structures of man but it appears to take dragonflies oftener than does the cliff swallow.

Northern Cliff Swallow, *Petrochelidon albifrons albifrons* (Rafinesque): 380 stomachs examined, 12 with adult dragonflies. Before the advent of white man this swallow built its mud jugs under overhanging cliffs and banks. In the eastern states it has adapted itself to the protection of overhanging eaves though in the western states it still uses cliffs. This change in the east has taken it away from streams. Its food is mainly insects of which small beetles are the largest item.

Purple Martin, *Progne subis subis* (L.): 210 stomachs examined, 65 with adult dragonflies. From these records the purple martin eats twice as many dragonflies as does any other species of the swallow family. Beal (1918) says of them, "dragonflies appear to be a favorite food of the martin. They were eaten every month except February and were contained in 65 stomachs, of which 7 held nothing else. Many were of the larger species, seemingly rather large morsels for the bird." The total for the season is 15.1% of the food, a percentage unusually large for Odonata and indicating that the martin hunts especially for them. The bank swallow is the only other species that eats enough dragonflies to warrant a separate record. Aquatic in their larval stage, dragonflies naturally stay about water or wet places, and as martins are likely to nest at a distance from water, to get them the birds must go to the haunts of the insects. Doolittle (1919) observed fifteen pairs of Martins feeding their young for some time entirely on dragonflies. (Widmann 1884).

Cuban Martin, *Progne cryptoleuca* Baird: 3 stomachs examined, each with one dragonfly. (No published records of food of Cuban martin found.)

Caribbean Martin, *Progne dominicensis* (Gmelin): Wetmore (1916) on the basis of 12 stomachs taken in Puerto Rico found 8.09% of the food to be dragonflies.

FAMILY CORVIDAE (crows, ravens, magpies, jays, nutcrackers, pinon jays.)

This family contains the brains of our North American bird fauna. The brain is so large that the skin has to be split up the neck to clean the head in making a skin of any of the species. After having watched American Magpies and the California Jay operate in accomplishing a fat living in a semidesert country one has great respect for their intelligence. Crows and blue jays are also almost as wise. Instances of behavior can be cited that suggest the presence of a very playful instinct and a sense of humor.

However, all the species tend to be rovers. They are on the hunt for the occasional bountiful dinner, whether fruit, grain, flesh of larger animals or insects. This roving habit brings Odonata into their diet only casually. In general the birds that prey most on dragonflies are those that remain closely associated with a dragonfly environment.

Because the crows, magpies and some of the jays are at times more harmful to farmers and fruit growers than they are beneficial, several of the species have been extensively studied by the Biological Survey and other agencies. The literature on such is extensive. (McAtee 1913).

There are no Biological Survey records of dragonflies taken by the white-necked raven, *Corvus cryptoleucus* Couch, of the southwestern states, of the Clarke nutcracker, *Nucifraga columbiana* (Wilson) nor of the pinon jay, *Cyanocephalus cyanocephalus* (Wied.). However, few stomachs of these have been taken. (Bent 1946; Bull. 141; Forbush 1927; Henderson 1927; Kalmbach 1927).

Northern Blue Jay, *Cyanocitta cristata cristata* (L.): 680 stomachs examined, 5 with adult dragonflies, one with a nymph. The blue jay is a bird of the woods, a heavy eater of acorns, beech nuts, and other large seeds, and thus does not often contact dragonflies.

The fifteen or so other northern and western true jays are also birds of the woods where dragonflies are seldom met with. Probably any jay would eat a dragonfly if the two met. In general the jays use smaller foods but have the omnivorous habits of the magpies and crows.

American Magpie, *Pica pica hudsonia* (Sabine): 560 stomachs examined, 18 with remains of Odonata, 7 of these containing anisopterous adults, one with 2 and another with 3 while 2 contained zygopterous adults. Six stomachs contained nymphs, one with 100 anisopterous nymphs and another with 35 zygopterous nymphs. From the large numbers found in some of the stomachs the magpie must make it a point to eat as many as are available when they are found. They are not picked up accidentally as with many birds.

The magpie has the crow habit of cruising about over an enormous area but usually in pairs or family flocks. When it does find food in its wanderings it stops and cleans up the local supply and returns on the next day to check. It is omnivorous but eats many insects in season. (Kalmbach 1927)

Yellow-billed Magpie, *Pica nuttalli* (Audubon): 25 stomachs examined, 3 with adult Anisoptera but one of these contained 12 and another 13 dragonflies. This is a bird of the Californian foothills of the Sierra where it nests along streams and uses the inner bark of cottonwoods as a feature of its nest. It may have the western robin habit of hanging about water and catching dragonflies as they emerge in numbers. (Kalmbach 1927).

American Raven, *Corvus corax sinuatus* Wagler: 20 stomachs examined, 2 with Odonata, one with an anisopter the other with a zygopter. The raven is a carrion eater feeding more often on dead fish than anything else but eats any kind of animal food. It is too large and slow to catch many really active Odonata.

American Crow, *Corvus brachyrhynchos* Brehm: Over 2,000 stomachs examined, only 19 of which contained Odonata. Four contained adult Anisoptera, 5 contained adult Zygoptera, one with 5 individuals

and another with 16. Seven contained anisopterous nymphs, one stomach containing 40. Evidently crows eat dragonflies freely when they are easily taken but are too slow and large to get many adults. (Gardner 1926; Hering 1936; Kalmbach 1940).

Fish Crow, *Corvus ossifragus* Couch: One observation by Miss Phoebe Knappen (1933) of the Biological Survey. The fish crows were eating dead Odonata on the beach. It is a bird of the coasts of the southeastern states.

FAMILY PARIDAE (titmice, chickadees)

In our area the species of this family tend to be winter visitants as the majority of the forms breed from the northern tier of states north or in the west on the crests of the higher mountains. They search the trunks, limbs and twigs of trees for small insects. When dragonflies are found on trees they are either on the outer leaves in the sunshine or are chilled or sleeping on the trunk.

The food of the Paridae is very much like that of the nuthatches, if anything, containing more vegetable matter in the form of buds and seeds. The feeding habits are similar except that the Paridae usually search small branches as well as trunks. The taking of Odonata is purely accidental. (Bent 1946; Forbush 1929; Henderson 1927).

Black-capped Chickadee, *Penthestes atricapillus atricapillus* (L.): 660 stomachs examined, 2 with adult dragonflies.

The black-capped chickadee is the only species of the twenty or more forms of this family which has records of having eaten Odonata.

(The A. O. U. List next records three families, the nuthatches (Sittidae), the creepers (Certhiidae) and the Pacific Coast family, the wren-tits (Chamaeidae) none of which have any records of having used dragonflies for food. These are mostly small birds on the borderline of being smaller than the birds that may use dragonflies as food. The nuthatches and creepers are tree-trunk birds. Only rarely are dragonflies, and then in a chilled condition, found on tree trunks.)

FAMILY CINCLIDAE (dippers, water ouzels)

Dipper, Water Ouzel, *Cinclus mexicanus unicolor* Bonaparte: 60 stomachs examined, 1 with a dragonfly. This curious bird feeds on larvae of water insects, small fish, crayfish and on insects floating on the surface of the streams it inhabits.

One of the thrills of dragonfly hunting in the west was given by the ouzels or dippers on the mountain streams. These slate gray thrush-like birds were generally found in pairs in the shadowy gorges where, bobbing like sandpipers, they skipped from rock to rock or ran along the stream edge in their hunt for insects or other aquatic animals. They are said to have the remarkable ability of walking and swimming under the water. The writer has observed several pairs in the Coast Ranges of California but has not seen any so aquatic. The mossy nest was usually on a nearby wet cliff, or even under a water fall.

In western streams there are few dragonflies in the swifter parts preferred by ouzels and such as are found in such swift waters are cordulegasters, gomphines or aeshnines all of which are large even among the Anisoptera or larger dragonflies. The smaller dragonflies, Zygoptera, with the exception of some argias, are found in abundance on the lower, slower portions of the mountain streams which are not frequented by ouzels. The stomach examinations show that they feed on the larvae of Trichoptera, Neuroptera, Ephemerida and on small insects floating on the water. Thus, while they live in a dragonfly habitat of a kind, they are adapted by size to smaller insects than the usual large, swift dragonflies that live in this very special habitat. (Henderson 1927).

FAMILY TROGLODYTIDAE (wrens)

Records show that the wrens are almost wholly insectivorous in their food habits. They show also that these very nervous and active birds usually catch slow insects, Orthoptera, Coleoptera, Hemiptera, caterpillars, and ants. By other birds fast insects are more often taken on the wing so the wrens which seldom thus catch insects, capture only the slower forms. The dragonflies recorded may have been taken in early or late hours when chilled and settled on vegetation. Thus only seven of the twenty or more forms of wrens in our area have records of having taken dragonflies. Two of these are marsh birds nesting in emergent vegetation in the very midst of the greatest dragonfly population and though insectivorous one shows only 3% of stomachs with Odonata and the other 5%. The wren's habit of feeding while perched appears to be the explanation of the lack of dragonflies. (Beal, McAtee & Kalmbach 1941; Forbush 1929; Henderson 1927).

House Wren, *Troglodytes aedon* Vieillot: 390 stomachs examined; 1 with an adult dragonfly. See Henderson (1927) for many references to the obnoxious feeding and fighting habits of the house wren.

Eastern Winter Wren, *Nannus hiemalis hiemalis* (Vieillot): 230 stomachs examined, 3 with Odonata, one of which was a larva: a swamp thicket bird but probably too small to care for even many small Zygoptera. (Barrows 1912 pp. 675-677 for habits.)

Bewick's Wren, *Thryomanes bewicki bewicki* (Audubon): 250 stomachs examined, 2 with adult Odonata.

Carolina Wren, *Thryothorus ludovicianus ludovicianus* (Latham): 415 stomachs examined, 2 with adult dragonflies.

Long-billed Marsh Wren, *Telmatodytes palustris palustris* (Wilson): 415 stomachs examined, 13 with adult Odonata. Ground and tree insects mostly. (Knappen 1933, p. 452.)

Short-billed Marsh Wren, *Cistothorus stellaris* (Naumann): 100 stomachs examined, 5 with adult dragonflies. (Little published data on stomach contents: Howell 1924).

Common Rock Wren, *Salpinctes obsoletus obsoletus* (Say): 60 stomachs examined, 1 with an adult dragonfly. Knowlton and Harmston 1942 found 3

Odonata in 88 stomachs and give a detailed list of the very miscellaneous insects used by this bird.

FAMILY MIMIDAE (mockingbirds, catbird, thrashers)

Birds of this family are highly insectivorous eating the larger and slower forms of insects which they capture while the bird is on its feet. They are also very fond of berries and other small fruits, which constitute over 50% of their food. Dragonfly catches appear to be accidental and are probably sleeping or chilled specimens hanging under trees and bushes. The mocking bird is one of similar behavior in the southern states but is more a tree than a bush inhabitant. (Beal 1915b; Forbush 1929; Henderson 1927).

Mockingbird, *Mimus polyglottos polyglottos* (L): 500 stomachs examined, one with a dragonfly. (Knappen 1933).

Catbird, *Dumetella carolinensis* (L.): 690 stomachs examined, 9 with adult dragonflies, one stomach containing 12. The catbird is more of a bush bird than the mocking bird which may bring it more often in touch with dragonflies along bushy streams. (Gabrielson 1913).

Besides the eastern brown thrasher there are recognized nine western thrashers about the food of which less is known. See Kennedy (1911, 1912). While the thrashers are highly insectivorous they are birds of the thickets of high open land where they contact few dragonflies.

Brown Thrasher, *Toxostoma rufum* (L.): 660 stomachs examined, 2 with adult dragonflies: a bird of open forest on ridges as compared with the catbird in bushes frequently in lower areas. (Gabrielson 1912).

FAMILY TURDIDAE (solitaire, thrushes, robins, bluebirds)

The thrushes and robins are ground feeders except for some fruit taken at times. They catch a very mixed lot of ground animals including many larvae and worms of various kinds. Except for an occasional opportunity of taking dragonflies emerging, as cited below, they probably catch few insects of this order. Ordinarily dragonflies are accidental catches.

The blue bird appears to catch somewhat more active insects which may account for the greater number of Odonata. Also it feeds more often in low trees and bushes where dragonflies may be roosting in early morning. In February and March, 1895, it was nearly exterminated by a late cold spell but has recovered its numbers (Barrows 1912). As a boy the writer gathered dead bluebirds and chimney swifts in the family cow pasture in Spencer County, southwestern Indiana. (Beal 1915a; 1915b; 1915c; Forbush 1929; Henderson 1927).

American Robin, *Turdus migratorius* L.: 1230 stomachs examined, 5 with adult dragonflies. (Beal 1915a; Howell 1942; Jenks 1859).

The Western Robin (*Turdus migratorius propinquus* Ridgw.) at times as observed on Donner Lake, California, is a distinct enemy of dragonflies. On the shores of Donner Lake a flock of robins patrolled the beach and caught many emerging gomphine dragonflies of the species *Ophiogomphus morrisoni* Selys. They caught the tenerals as these crawled across the beach from the edge of the water where they had emerged from the larval skins. Apparently the robins were taking little else. (Kennedy 1917; A. C. Howell 1942).

Olive-backed Thrush, *Hylocichla ustulata swainsoni* (Tschudi): 403 stomachs examined, 2 with adult Odonata, one with a larva.

Gray-cheeked Thrush, *Hylocichla minima aliciae* (Baird): 111 stomachs examined, one with an adult dragonfly; as with other thrushes a ground feeder on insects and other invertebrates: breeds in northern Alaska and Canada.

Eastern Bluebird, *Sialia sialis sialis* (L.): 855 stomachs examined, 4 with adult dragonflies: a bird of orchards and open bushy areas. Any dragonflies eaten are strays. (Beal, McAtee & Kalmbach 1941; McAtee & Kalmbach 1927).

Townsend's Solitaire, *Myadestes townsendi* (Audubon): 41 stomachs examined, one with a dragonfly. This is a bird of the highest mountain ranges living at boreal elevations where few dragonflies occur on the cold snow-water streams. According to Florence Merriam Bailey (1902), they may breed in the high transition zone, even into the high mountains of northern Mexico, but in central California at 7,900 feet.

(We next come to the Sylviidae, true warblers, gnatcatchers and kinglets and the Motacillidae, wagtails and pipits, two native families which are in most species too small to be tempted by insects as large as dragonflies. Usually they are birds of the foliage and smaller branches of the tree tops. They are birds of north of the Canadian border during the breeding season for which reason their summer diet has not been studied by the Biological Survey.)

FAMILY BOMBYCILLIDAE (waxwings)

The waxwings are interesting because in the season between periods of rearing young they are very gregarious and may be viewed as being semi-social. During the breeding season they lead a more nearly family-life, each pair of parents with interest in its own nest. It is at this time when with more nearly solitary habits and the necessity of insect food for their young that dragonflies may enter the waxwings diet, incidental to the taking of any easily available insects. Social tendencies (such as occur in waxwings during the migratory and winter seasons) in birds which *do not live* on the water will tend to keep individual socii away from the water, will help hold them on the land areas with their fellow land-socii. Also the social season is the off season for dragonflies.

(There are no records of the bohemian waxwing (*Bombycilla garrula pallidiceps* Reichenow) having eaten dragonflies. It breeds from lower central Canada north and may take occasional Odonata when feeding its young. (Forbush 1929; Henderson 1927)).

Cedar Waxwing, *Bombycilla cedrorum* Vieillot: 225 stomachs examined, 3 with adult dragonflies. In this series of stomachs one contained a stonefly and 5 contained mayflies. This species is mainly an eater of wild fruits and in the winter an eater of frozen fruits but it feeds its nestlings on insects largely. (Beal 1902).

(The silky Flycatchers (Ptilogonatidae) are a family of one species in the valleys of southern California and Mexico. We found no record of their having eaten dragonflies.)

FAMILY LANIIDAE (shrikes)

It is interesting to compare the shrikes with the sparrow hawks, and other small falcons. The two groups are in the same order of size, the same order of density of population, the same geographic distribution, the same general taste for prey of the size of mice, grasshoppers and the larger dragonflies. The small hawks take a considerable number of large dragonflies. The shrikes take few. The hawks take Odonata when the latter are on the wing in open places where large dragonflies prefer to fly. The shrike more often is a hunter in the undergrowth and brush where dragonflies seldom occur. The northern shrike, *Lanius borealis borealis* Vieillot, nests far to the north and does not meet adult Odonata during its winters in the States. (Beal & Judd 1898; Forbush 1929; Henderson 1927).

White-rumped Shrike, *Lanius ludovicianus excubitorides* Swainson: 303 stomachs examined, 3 with adult dragonflies. This is a general feeder on small land animals, mice, small birds, lizards, insects, etc. From the records most of the insects eaten are conspicuous and large, such as crickets, locust, caterpillars and ground beetles. (Beal & McAtee 1922; Knowlton & Haimston 1944; Tate 1925.)

California Shrike, *Lanius ludovicianus gambeli* Ridgway, a western form of the white-rumped shrike, the Survey records for which are included in *excubitorides* in the above. It is noticeably associated in the field with the sparrow hawk (Beal 1907), yet in hunting over similar ground the sparrow hawk takes many more Odonata. (Bryant 1914b).

FAMILY STURNIDAE (starlings and mynahs)

Because of the success in the United States of the immigrant starling we would not expect it to be a feeder on dragonflies. Such are too scarce an item on nature's bounteous table for a successful mass population development. Stomach studies show that the starling had 2749 chances out of a total of 2750 of not getting noticed in this article. Having been born with the stainless steel spoon of success in its mouth it entered our list on that one chance in 2750. The one dragonfly recorded against it may be interpreted as evidence of the starling's great adaptability.

We need not fear the extermination or serious reduction of Odonata by successful immigrant birds. Such come from Eurasia where, because of the greater size of the continental area, bird-evolution is one geological age ahead of bird-evolution in North America. (See Taverner 1935 on shape of continents and bird evolution.) Such successful species are advanced evolutionary types. They are gregarious almost to a social life. They have a broad and catholic taste which gives access to a great variety of foods permitting them to live well on that which is most abundant locally. Dragonflies are too small an item to receive the attention of such a species. See remarks on the social factor under the waxwings and the martins.

Starling, *Sturnus vulgaris vulgaris* L.: 2,750 stomachs examined, one with one anisopterous adult. (Bready 1929; Judd 1931; Lindsey 1939; Kalmbach 1931).

FAMILY VIREONIDAE (vireos)

The vireos are small shrikes, or perhaps the shrikes are large vireos. The difference in habits between the two families is largely due to the difference in size between a vireo and a shrike. The large shrikes are bushwhackers that include small vertebrates (birds, mice, lizards) in their diet of fairly large insects. The small vireos are more generally tree species where they search the foliage and smaller branches for any insects whatsover. Caterpillars, large bugs and small beetles are the main items in their diet. Because they take many ladybird beetles and parasitic Hymenoptera the value of the vireos to the agriculturist has been questioned. It is a group the Survey has studied rather thoroughly. From the records following, dragonflies are accidents in the vireo diet, probably an occasional chilled individual roosting in the foliage of a tree.

The nine other recognized forms of vireo in our area (not listed as dragonfly eaters) have no records of having taken Odonata, partly because their ranges are limited and less is known concerning them. Obviously the family as a whole prefer caterpillars and Hemiptera but are predators on many kinds of insects which they catch in bushes and tree tops. (Chapin 1925; Forbush 1929; Henderson 1927; McAtee 1907).

White-eyed Vireo, *Vireo griseus griseus* (Boddaert): 245 stomachs examined, 10 with dragonflies, 6 of which were Zygoptera. The white-eyed vireo lives about water more than do the other species. Its food is 88% animal of which 20% is caterpillars, 20% Hemiptera, 7% Hymenoptera, 4% Diptera, 3.5% Arachnida. Barrows (1912, p. 575) points out that the nesting area of bushes in swampy areas is similar to that of the yellow-breasted chat. Habits are curiously alike. Our data is on only 25 stomachs of the chat but those have the same proportion of Odonata as this vireo.

Hutton's Vireo, *Vireo huttoni huttoni* Cassin: 75 stomachs examined, one with a dragonfly. The food of the bird is 98% animal of which 8% is coccinellid beetles, 12% caterpillars, 46% Hemiptera, 6% Hymenoptera, 3% Diptera, 2% Arachnida.

Bell's Vireo, *Vireo belli belli* Audubon: 60 stomachs examined, one with a dragonfly. The food of the

Bell's vireo is 99% animal of which 15% is caterpillars, 34% Hemiptera, 15% beetles.

Yellow-throated Vireo, *Vireo flavifrons* Vieillot: 155 stomachs examined, 5 with dragonflies, 4 of which were Anisoptera. The food of this species is 98% animal of which 23% is caterpillars, 19% other Lepidoptera, 23% Hemiptera, 5% Hymenoptera, 7% Diptera and 2% Arachnida. In nesting the yellow-throated vireo prefers heavy hardwood timber but also oaks in wet ground (Barrows, 1912, p. 572). The dragonflies suggest wet areas.

Blue-headed Vireo, *Vireo solitarius solitarius* (Wilson): 325 stomachs examined, 9 with dragonflies. The food of the red-eyed vireo 85% is animal of which 23% is caterpillars, 30% Hemiptera, 7% Hymenoptera, 4% Diptera, 2.63% Arachnida. Hunting areas and nest sites similar to those of the yellow-throated vireo but nests nearer the ground.

Red-eyed Vireo, *Vireo olivaceus* (L.): 660 stomachs examined, 14 with adult dragonflies. Of the food of the red-eyed vireo 85% is animal of which 32% is caterpillars, 11% Hymenoptera, 4.5% Diptera and 4% Arachnida. A widely spread woods bird with fewer Odonata to its credit, it is repeatedly credited as our most beneficial vireo.

Warbling Vireo, *Vireo gilvus* (Vieillot): 350 stomachs examined, one with a dragonfly. The food of this species is 94% animal of which 35% is caterpillars, 17% Hemiptera, 6% Hymenoptera, 9% Diptera and 2% Arachnida: A tree bird with a low take of dragonflies.

FAMILY COMPSOTHLYPIDAE (wood warblers)

From the records following below less than 10% of the species of the wood warblers have been found to catch Odonata. Warblers are in general small birds of the tree tops though a few, such as the yellow-breasted chat and Maryland yellow-throat, live low in thickets (Chapman 1937, Height of nests). While highly insectivorous the majority do not meet many small dragonflies in the dense foliage of tree tops. Such meetings are accidents and account for the occasional dragonfly taken. Except for the yellow-breasted chat the majority of the warblers are smaller than the usual dragonfly eating bird. (Chapman 1937; Forbush 1929; Henderson 1927; McAtee 1907.)

Black and White Warbler, *Mniotilta varia* (L.): 21 stomachs examined, 2 with dragonflies. This species takes more Odonata than other warblers. It hunts more often over the bark of trunk and large limbs where cold-bound dragonflies often rest.

Yellow Warbler, *Dendroica aestiva aestiva* (Gmelin): 120 stomachs examined, 3 with dragonflies. Food of caterpillars, beetles, miscellaneous minute insects with 6% spiders. (Brigglestone 1913).

Audubon's Warbler, *Dendroica auduboni auduboni* (Townshend): 390 stomachs examined, one with a dragonfly; a western mountain species.

Black-throated Gray Warbler, *Dendroica nigrescens* (Townshend): 11 stomachs examined by the Survey, one with a dragonfly. A western species. (No references on food.)

Maryland Yellow-throat, *Geothlypsis trichas trichas* (L.): 125 stomachs examined, one with a dragonfly larva. This species is partial to thickets along streams and the larva had probably crawled up to emerge. This is a surprise record. The Maryland yellow-throat is an abundant bird in humid bushy areas, a southern blackberry-thicket bird. Its tastes and size probably enter in: it avoids large hard Hemiptera but uses soft caterpillars.

Yellow-breasted Chat, *Icteria virens virens* (L.): 25 stomachs examined, one dragonfly, an Anisopter. As the chat is a giant among warblers it might easily catch an Anisopter which had strayed into the bushes. See note on white-eyed vireo.

FAMILY PLOCEIDAE (weaver finches)

The English sparrow, long placed in the Family Fringillidae with our less aggressive North American sparrows has recently been shown through a study of its anatomy by Peter P. Sushkin (1927) to belong to the family of weaver finches which are birds of a more generalized behavior, greater vigor and aggressiveness, more social development and greater reproductive ability. As with other successful immigrant birds, such as the starling, the English sparrow comes from Eurasia where because of the great area it has been able to reach an evolutionary level about one geological age in advance of the majority of native North American birds. As with the starling it makes use of any abundant local supply of food. As with the starling this habit of life tends to tie it to man's works in agriculture, and in storage and transportation of agricultural products as man is the greatest producer of foods used by the English sparrow. The tie-up with man and his food production tends to hold the English sparrow away from dragonfly environments which are usually untouched areas yet in a relatively primitive condition. See remarks on the martin and the starling for the other factors in this problem. (Barrows 1889).

English Sparrow, *Passer domesticus domesticus* (L.): 1,500 stomachs examined, 4 with adult dragonflies. The English sparrow has been one of the birds very much studied by the Survey. For the extensive literature we refer the reader to Henderson (1927).

FAMILY ICTERIDAE (blackbirds, orioles, bobolink, meadow larks)

Of the twenty or more forms of blackbirds and meadowlarks found north of Mexico only two are regular eaters of dragonflies and then only in the nesting season. These are the yellow-headed blackbird and the thick-billed redwing. The others, as shown in the following notes, take dragonflies only accidentally as would any land insectivorous bird. Much depends on the nesting site as it is then that they are most insectivorous. Those that nest entirely away from the water catch dragonflies only occasionally.

The seven forms of oreoles found in our area are tree birds and have no records of having eaten dragonflies. (Beal 1900: Forbush 1927; Henderson 1927).

Bobolink, *Dolichonyx oryzivorus* (L.): 315 stomachs examined 3, with adult dragonflies. Beal's (1898) report shows 90% of insect food for the bob-o-link in June and 5% in September. Out of the nesting season the food is mainly seeds and grain. This bird nests in meadows in the higher of which few dragonflies are found. In the lower marshy meadows that are dry in the late fall, dragonflies are usually on the wing in late summer and fall after the nesting of the bob-o-link is over.

Meadowlark, *Sturnella magna* (L.): 1,400 stomachs examined, one with an adult dragonfly. This is strictly a dry meadow or prairie bird. The meadowlark does not take insects on the wing and is slow on its feet so that dragonfly catches are gastronomic accidents in its life. Probably our list of birds would be doubled, if for each species of American bird as many stomachs had been examined as have been for the meadow lark. Its food, of which 74% is animal matter, is largely composed of the larger, slower ground insects. It has special economic value in the large item of grasshoppers, and other Orthoptera in its diet. One Mormon cricket campaign at Adrian, Washington, in 1919 (Burrill 1920) was abandoned because the meadowlarks flocked in and did the necessary work of cleaning up the crickets.

Thus the meadowlark, while an eater of insects as large or larger than dragonflies, favors high, dry ground where Odonata seldom stray. Also they are slower in action than the successful catchers of dragonflies. (Bryant 1914; Knowlton & Maddock 1943).

The blackbirds are heavy grain eaters in the more southern fields of irrigated rice, milo, barley, etc. Here they raid low areas in great flocks in late summer, and at such times are near or in a dragonfly environment. Their take is above that of birds which catch Odonata accidentally. The tricolored, brewer, redwing, thick-billed and yellow-headed were the worst offenders. The yellow-headed breeding in cattails over water, is one of the three species of birds most interested in Odonata as food for the young. They are the species most closely associated with a fresh-water marsh environment.

Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Bonaparte): 262 stomachs examined, 67 with remains of dragonflies. Two contained Odonata nymphs.

All blackbirds except the bronzed grackle love low wet ground. Few Odonata appear in the records against them except in the case of the yellow-headed blackbird which nests in emergent cattails. They use teneral Odonata. All species feed standing and use slow insects. Probably all have the poor vision of short-necked ground-feeding birds.

The following is from the writer's observations among the cattail-bordered ponds of the Yakima Valley, Washington. The yellow-headed blackbirds nest over the water in the cattails and feed their young almost exclusively on aquatic insects, taking these as they emerge from the water in vast numbers coincident with the nesting season of the birds. They confine their foraging to the emergent vegetation of the ponds and marshes and practically live on aquatic insects at this season. After the young can fly they forage more widely over the surrounding higher ground. The dragonfly nymphs found in their stomachs were probably taken as they crawled up to emerge. (Fautin 1940, 1941).

Several birds were shot and their stomachs on examination contained wads of dragonfly wings, mostly partially expanded zygopterous wings. This bird thus nests in the cattails over the water and rears its young at the peak of dragonfly emergence. The desert days are always bright so that dragonflies can be depended on to emerge daily in large numbers. It is one of the few birds in our area that the writer feels is a direct and important enemy of dragonflies, at least during the season of emergence. The others are the western robin, the purple martin, and Franklin's gull. Beal (1900) credits nestlings of the yellow-headed blackbird with 43% of dragonflies in their food.

It would be interesting to map the nesting areas of this species and see if there is any correlation between nesting area and abundance of Odonata in the cattails. Western ponds vary greatly in the number of Odonata produced. Those with insect eating fish produce noticeably fewer than do the more temporary ponds which become dry enough each fall to keep the fish population low.

Eastern Red-wing, *Agelaius phoeniceus phoeniceus* (L.): 1,000 stomachs examined, 30 with dragonflies, 22 of which contained adults. As the red-wing tends to be a marsh bird, the nymphs were probably taken while crawling out to emerge. (Allen, A. A. 1914; Knappen 1933).

Thick-billed Red-wing, *Agelaius phoeniceus fortis* Ridgway: Beal (1900) records the thick-billed red-wing as giving its young dragonflies to the amount of 9.84% of the total food.

Tricolored Red-wing, *Agelaius phoeniceus tricolor* (Audubon) (?): A redwing at Sunnyside, Washington, in the lower Yakima Valley which in F. M. Bailey's "Handbook of Birds of the Western United States" did not key out satisfactorily to either the bicolored red-wing or the tricolored red-wing was observed on the writer's dragonfly collecting trips. It was studied about the same Yakima Valley ponds as noted for the yellow-headed blackbird but no evidence was gathered that they were feeding their young on a noticeable number of dragonflies. Several were shot but these were feeding on land insects, caterpillars, moths, beetles, etc., and were observed feeding the same to their nestlings. (Bryant 1914).

Rusty Blackbird, *Euphagus carolinus* (Muller):

130 stomachs examined, one with an adult and one with a nymph. According to Brimley (1919) these feed in marshes in the spring. The rusty blackbirds "are never so happy as when their feet are wet," Barrows (1912, p. 454). They frequent the shallows of pools and streams; water beetles are a large item of food which contains more animal matter than that of other blackbirds (53%). Why few Odonata?

Brewer Blackbird, *Euphagus cyanocephalus* (Wagler): 725 stomachs examined, 19 with adult dragonflies. As this bird nests in low bushes and usually about water it is surprising that it does not take Odonata oftener. Beal (1910, p. 61) credits it with many caterpillars in its diet.

Boat-tailed Grackle, *Cassidix mexicanus major* (Vieillot): 250 stomachs examined, 5 with adult dragonflies. According to Beal (1900) it is a heavy feeder on grasshoppers, wild fruits and grains but Brimley states that in North Carolina it is a coast bird feeding on shrimps, crabs, etc., washed up on beaches and is rarely found as much as six miles inland. Brimley, *et al.* (1919) was a careful observer as noted by the writer on joint collecting trips around Raleigh, N. C. (Beal, McAtee & Kalmbach 1941).

Bronzed Grackle, *Quiscalus quiscula aeneus* Ridgway: 2,600 stomachs examined, 3 with Odonata, 2 of the stomachs containing nymphs. This is a bird that usually nests in the tops of the tallest trees of heavy woods and feeds in high open land. It apparently does not come into the dragonfly habitat to any extent. See notes under yellow-headed blackbird. (Beal 1894).

Eastern Cowbird, *Molothrus ater ater* (Boddaert): 700 stomachs examined, one with an adult anisopterous dragonfly. This is an upland bird that has the habit of riding on the backs of cattle and of feeding on the insects the cattle flush. It does not feed its own nestlings. (Beal 1900).

(The orioles had no records of dragonflies eaten by them. Our eastern species, the Baltimore and orchard orioles, are birds of tall trees above the zone of usual dragonfly flight. Bullock's oriole which nests in trees along desert streams in the West should be expected to pick up Odonata occasionally.)

FAMILY THRAUPIDAE (tanagers)

The five forms of tanagers are insect and fruit eaters but live in high trees, an area little used by dragonflies. (Forbush 1929; Henderson 1927).

Western Tanager, *Piranga ludoviciana* (Wilson): 54 stomachs examined, one with a dragonfly.

Scarlet Tanager, *Piranga erythoromelas* Vieillot: 330 stomachs examined, 3 with adult Odonata.

FAMILY FRINGILLIDAE (finches, sparrows, grossbeaks, crossbills, etc.)

The few records of this family of over one hundred and twenty forms found north of Mexico indicate how little the family as a whole is concerned with the eating of dragonflies. While all are essentially seed-eaters, the majority feed their nestlings on insects. It apears to be a group of species of the proper size of body, neither too large nor too small, and to be highly insectivorous during the nesting season. However, at other times they are seed eaters and as is the case with other herbivorous birds are less speedy in general reactions and probably seldom take food on the wing. This dullness of both senses and muscular reactions associated with herbivorous habits, perhaps because there is little chance of plant food escaping, may be the factor that allows swift insects to pass by untouched. Records show that they tend to eat the slower insects, Coleoptera, Orthoptera, and Lepidoptera, of the later usually caterpillars and pupae. (Forbush 1929; Henderson 1927; McAtee 1908).

Redbird, Eastern Cardinal, *Richmondena cardinalis cardinalis* (L.): 550 stomachs examined, 3 with dragonflies. As the redbird is one of the largest of the finches it might have been expected to have taken dragonflies oftener. In the author's backyard the redbird is noticeably a slow bird. (McAtee 1908).

Vesper Sparrow, *Pooecetes gramineus* (Gmelin): 260 stomachs examined, one with a dragonfly.

Slate-colored Junco, *Junco hyemalis hyemalis* (L.): 560 stomachs examined, 2 with dragonflies.

Brewer's Sparrow, *Spizella breweri breweri* Cassin: 65 stomachs examined, one with dragonfly. A western desert sparrow.

Song Sparrow, *Melospiza melodia* (Wilson): 750 stomachs examined, 3 with dragonflies. This species of all sparrows would be expected to take dragonflies oftenest as it has the habit of nesting close to or along streams. It is the best evidence of how few Odonata are eaten by birds of this family as it is the species most regularly in a dragonfly environment. (Haldeman 1913).

TAXONOMIC INDEX TO DRAGONFLY-EATING BIRDS, NUMBER OF STOMACHS PER SPECIES AND NUMBER OF STOMACHS WITH DRAGONFLIES

The following lists show that the use of dragonflies by birds is a primitive habit. The heavy consumers of dragonflies are in the first half of the list, about 80 species, which excepting the hawks are mostly associated with water. Nearly all nymph eating birds fall in the group, the grebes, herons, ducks and shore birds. In the higher half of the list only the belted kingfisher and the western robin prefer nymphs to adults, but the belted kingfisher by present classification is a modern bird which has evolved in reverse and has become a diving waterfowl with the habits and tastes of more primitive birds. Can evolution go into reverse among vigorous predators as well as among feeble parasites, if the taxonomists have interpreted the evolutionary data correctly? (*Vide postea*).

The present ornithological classification of the hawks and falcons places them in the lower half of the list, but their habits of feeding on the wing limit

their take to adult dragonflies except the red-shouldered hawk which tends to be a scavenger on the ground where it captures an occasional nymph.

Nearly all of the species in the more primitive half of the list retain the reptilian habit of nesting on the ground with a few exceptions which nest in trees such as the herons, wood duck, solitary sandpiper, and the hawks (excepting the marsh hawk which nests on the ground).

The latter half of the list, roughly from the cuckoos to include the Passeriformes, use only adult dragonflies, and use these very seldom. Probably all catches in the higher half are from accidental contacts except the martins, the two marsh wrens and two blackbirds (yellow-headed and perhaps the thick-billed). These apparently choose dragonflies when available particularly when feeding young. They use adults only, so are physiologically in the upper half of the bird series.

We wish to call the attention of ornithological taxonomists to the odd and exceptional placement of the belted kingfisher among the birds of the higher series. (See the following list.) The kingfisher has probably been placed so on his osseous anatomy. If so only one item of his physiology agrees with his placement anatomically.

He lives in holes in vertical clay and loess banks which in the verticalness of the bank are peculiar to swallows in the upper series of birds. Puffins and some murres dig holes in the ground as do Florida and western ground owls but holes in more horizontal surfaces, a somewhat different behavior. As a bird of the lower series of primitive habits he is a fish-eating diving water-fowl. In nesting he avoids broad-leaved trees of geologically recent forests and the prairies of even more recent times. The kingfisher is so perfectly attuned to his aquatic, fish-eating habits that he must have had a geologically long period back of his present repertoire of habits to have permitted their development to present perfection. His dragonfly-nymph eating habits are strictly those of waterfowl of the more primitive lower series. His voice is that of the lower series and so probably the structure of his syrinx. His colors and dense plumage are in the lower series. Even two toes are syndactyl (webbed?). Is it possible that the kingfisher is another misplaced "English Sparrow" where habits were for so long ignored?

On the side of the dragonflies, if Darwinian evolution would operate precisely and eliminate the present "living primitive" birds, the dragonflies would prosper as far as modern birds are concerned. They survived the cold weather of the Permian, the small, toothless, probably warm-blooded, bird-like pterosaurs of the Cretaceous and are at present out-evolving modern birds, the birds of broad leaved forest trees and dry grass lands. (But the dragonflies still have their worst enemies, fresh-water fish.)

The taxonomists' listing of "primitive" and "modern" birds is deceptive in our arguments because, if arranged on a Lamarckian "phylogenetic tree," the present-day so-called primitive birds would occupy

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
Grebes					
111	Holboell Grebe	50	1	..	1
111	Horned Grebe	156	6	3	3
111	Eared Grebe	35	6	6	..
111	Pied-bld. Grebe	196	23	24	1
111	Antillean Grebe	1	1	2	..
Herons					
112	Gt. Blue Heron	125	29	10	19
112	Snowy Egert	20	5	..	5
112	La. Heron	60	10	1	9
112	Little Blue Heron	45	27	38	7
112	Green Heron	215	80	21	59
112	Bl. crown N. Heron	100	12	7	5
112	Yel. crown N. Heron	110	1	..	1
112	Amer. Bittern	125	29	12	17
112	Least Bittern	100	41	25	16
113	W.-faced Gl. Ibis	15	2	2	..
113	White Ibis	20	1	1	..
River Ducks					
113	Mallard Duck	2,010	197	126	71
113	Black Duck	645	25	20	5
113	S. Bl. Duck	52	10	6	4
114	Gadwall	410	5	3	2
114	Baldpate	270	2	1	1
114	Pintail	925	35	28	7
114	Gr. wgd. Teal	750	27	9	18
114	Bl. wgd. Teal	335	27	21	6
114	Cinnamon Teal	44	4	..	4
114	Shoveller Duck	88	3	2	1
114	Wood Duck	400	78	22	56
Sea Ducks					
114	Redhead	360	10	1	9
114	Ring-necked	655	92	8	84
114	Canvasback	380	10	8	2
115	Amer. Scaup	752	10	8	2
115	Lesser Scaup	1,155	176	26?	150?
115	Amer. Gold'-eye	175	8	5	3
115	Bufflehead	60	11	2	9
115	Ruddy Duck	55	4	?	?
Fish Ducks					
115	Hooded Mergans	50	18	10	8
115	Amer. Mergans	140	3	3	..
115	Red-br. Mergans	175	10	4	6
Hawks					
116	Miss. Kite	15	1	..	1
116	Sharp-shin. Hwk	925	2	..	2
116	Cooper's Hawk	215	2	..	2
116	Red-tailed Hwk	510	1	..	1
117	Red-shouldered Hwk	325	7	1	6
117	Broad-winged Hwk	90	1	..	1
117	Swainson's Hwk	30	2	..	2
117	Marsh Hawk	530	7	..	7
Falcons					
117	Aplomado Falcon	3	1	..	1
117	Pigeon Hawk	700	421	..	421
117	Sparrow Hawk	550	32	..	32
Turkeys					
118	Turkey	19	1	..	1
Cranes					
118	Sandhill Crane	16	2	2	..
Coots					
118	Coot	40	3	3	..
Shore Birds					
119	Killdeer	260	10	5	5
119	Antill. Killdeer	20	Odonata 3.92 %		
119	Golden Plover	100	4	4	..
119	Black-bellied Pl.	440	15	11	4
120	Woodcock	130	1	..	1
120	Wilson's Snipe	725	139	128	1
120	Eskimo Curlew	4	1	..	1
120	Bartramian Sandp.	200	1	..	1
120	Solitary Sandp.	7	1	1	1

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
120	Willet	230	16	10	6
120	Great. Yel. Legs	702	153	126	27
120	Lesser Yel. Legs	760	123	80	43
121	Knot	215	2	..	2
121	Pectoral Sandp.	104	3	..	3
121	Baird's Sandp.	45	7	1	6
121	Dowitcher	200	89	85	4
121	Long-billed Dowitcher	90	6	6	..
121	Stilt Sandpiper	15	3	3	..
121	Marbled Godwit	90	1	..	1
Stilts					
121	Amer. Avocet	55	3	3	..
121	Black-necked Stilt	70	9	9	..
Phalaropes					
121	Wilson's Phalarope	105	1	1	..
121	Northern Phalarope	150	3	..	3
Gulls, Terns					
122	Ring-billed Gull	50	4	..	4
122	Franklin's Gull	125	8	(other records nymphs)	
122	Bonaparte's Gull	140	1	..	1
122	Gull-billed Tern	7	3	..	3
122	Forster's Tern	60	2	2	..
122	Common Tern	116	a few	?	?
122	Arctic Tern	45	5	5	..
122	Black Tern	280	42	..	42
122	Black Guillemot	15	1	..	1
Cuckoos					
122	Yel.-bill. Cuckoo	350	10	..	10
122	Black-bill. Cuckoo	160	8	..	8
Owls					
123	Screech Owl	440	3	..	3
123	Pigmy Owl	50	1	..	1
Night Hawks					
123	Chuck-Will's-Widow	40	4	..	4
123	Nighthawk	315	22	..	22
123	Tex. Nighthawk	20	1	..	1
Swifts					
124	Chimney Swift	150	7	..	7
Kingfisher					
124	Belted Kingfisher	330	33	33	..
Woodpeckers					
124	Northern Flicker	700	2	..	2
124	Yel.-bellied Sapsucker	325	2	..	2
124	Downy Woodpecker	750	1	..	1
Flycatchers					
125	Kingbird	700	39	..	39
125	Ark. Kingbird	145	3	..	3
125	Cassins Kingbird	45	1	..	1
125	Scissor-tail Flyc.	130	1	..	1
125	N. crested Flyc.	265	26	..	26
125	Ash-throated Flyc.	90	6	..	6
125	East. Phoebe	365	11	..	11
125	Black Phoebe	340	67	..	67
126	Say's Phoebe	130	7	..	7
126	Yel.-bellied Flyc.	105	2	..	2
126	Alder Flyc.	155	9	..	9
126	Least Flycatcher	170	4	..	4
126	Wright's Flyc.	20	1	..	1
126	Western Flyc.	162	1	..	1
126	East. Wood Pewee	365	14	..	14
126	West. Wood Pewee	165	19	..	19
126	Olive-sided Flyc.	60	6	..	6
Swallows					
126	Tree Swallow	330	32	..	32
126	Bank Swallow	415	33	..	33
126	Rough-wgd. Swallow	135	4	..	4
126	Barn Swallow	135	4	..	4
127	N. Cliff Swallow	380	12	..	12
127	Purple Martin	210	65	..	65
127	Cuban Martin	3	3	..	3
127	Caribbean Martin	12	(8% of food drgfs.)		

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
Jays, Crows					
127	N. Blue Jay	680	6	1	5
127	Amer. Magpie	560	18	..	18
127	Yel.-billed Magpie	25	3	..	3
127	Amer. Raven	20	2	..	2
127	Amer. Crow	2,000	19	7	12
Chickadees					
128	Black-cap. Chickadee	660	2	..	2
Dippers					
128	Water Ouzel	60	1	..	1
Wrens					
128	House Wren	390	1	..	1
128	East. Winter Wren	230	3	1	2
128	Bewick's Wren	250	2	..	2
128	Carolina Wren	415	2	..	2
128	Long-billed Marsh Wren	415	13	..	13
128	Short-billed Marsh Wren	100	5	..	5
128	Com. Rock Wren	60	1	..	1
Mockers					
129	Mocking Bird	500	1	..	1
129	Catbird	690	9	..	9
129	Brown Thrasher	660	2	..	2
Thrushes					
129	Amer. Robin	1,230	5	..	5
129	Olive-backed Thrush	403	3	1	2
129	Gray-checked Thrush	111	1	..	1
129	East. Bluebird	855	4	..	4
129	Townsend's Solitaire	41	1	..	1
Waxwings					
130	Cedar Waxwing	225	3	..	3
Shrikes					
130	White-rumped Shrike	303	3	..	3
Starlings					
130	Starling	2,750	1	..	1
Vireos					
130	White-eyed Vireo	245	10	..	10
130	Hutton's Vireo	75	11	..	1
130	Bell's Vireo	60	1	..	1
131	Yel.-throated Vireo	155	5	..	5
131	Blue-headed Vireo	325	9	..	9
131	Red-eyed Vireo	660	14	..	14
131	Warbling Vireo	350	1	..	1
Wood Warblers					
131	Black and White Warbler	21	2	..	2
131	Yellow Warbler	120	3	..	3
131	Audubon's Warbler	390	1	..	1
131	Black-throated Gray Warbler	11	1	..	1
131	Maryland Yellow-throat	125	1	1	..
131	Yellow-breasted Chat	25	1	..	1
Weaver Finches					
131	English Sparrow	1,500	4	..	4
Blackbirds					
132	Bobolink	315	3	..	3
132	Meadowlark	115	1	..	1
132	Yel.-headed Blackbird	262	67	2	65
132	Eastern Red-wing	1,000	30	8	22
132	Thick-billed Red-wing (Beal.-Food of young 9.8% Odonata)				
132	Rusty Blackbird	130	2	1	1
133	Brewer Blackbird	725	19	..	19
133	Boat-tailed Grackle	250	5	..	5
133	Bronzed Grackle	2,600	3	2	1
133	Eastern Cowbird	700	1	..	1
Tanagers					
133	Western Tanager	54	1	..	1
133	Scarlet Tanager	330	3	..	3
133	Redbird	550	3	..	3
133	Vesper Sparrow	260	1	..	1
133	Slate-colored Junco	560	2	..	2
133	Brewer's Sparrow	65	1	..	1
133	Song Sparrow	750	3	..	3

tips of branches which would give them as much evolutionary modernness as is ascribed to perching birds which may be modern only in their more recent origin and adaptation to the protection of modern broad-leaved forests and the even more recent grasslands.

This brings us back to the arguments without much data: Why have "primitive forms" been preserved to the present when associated with an aquatic environment? Why do not evolutionists give more weight to the evolution of physiology in present forms where data are available. The writer feels certain that physiological evolution leads and is followed by anatomical adaptations. He has vivid evidence which he will present elsewhere.

SUMMARY: THE PROBLEM OF PREDATION IN THE GREATER PROBLEM OF DARWINIAN SURVIVAL OF SPECIES

As estimated we have reviewed the data obtained from probably 100,000 to 200,000 bird stomachs by the group of trained U. S. Biological Survey ornithologists. It has been a review of the activities of a continental bird fauna against a continental dragonfly fauna. It presents in broad aspect the problem of the Darwinian survival of a continental dragonfly fauna in the face of the assaults of a continental bird fauna.

Our general conclusion is that no species of dragonfly faces extermination by any species of bird or by any group of species of birds. For years in work on Odonata the writer has watched for evidence of the causes of the gradual evolutionary changes in odonate faunas and has become convinced that they are not a matter of predation by another animal group. (Gould 1871; McAtee 1912b, 1926, 1932).

The critical point in the problem of predator *versus* prey is that the predator has to meet the prey in the latter's own environment. In our specific example of the general problem, the bird has to meet the dragonfly as an egg or as a nymph in the water, or as an imago in the air. Because of this treble possible meeting of predator and prey our problem is the more vivid in analysis. Repetition by three environmental forms of meeting emphasizes the necessity of meeting. (Forbes 1882; Heape 1931).

We can narrow the problem by defining the much narrower environment of dragonflies as compared with the nearly continental spread of the bird fauna. With the exception of a few brackish water species of our coasts and inland salt waters as studied by Osburn (1916) and Pearse (1932) the dragonfly nymphs are confined to fresh water. (A few tropical species live in moist woods-loam or mud.) This restriction to fresh water confines North American dragonflies to streams, lakes, marshes, bogs, and swamps. The female dragonfly has to lay her eggs in fresh water or close enough to it (immediately adjacent) that the nymph can hatch from the egg in the water or on hatching can drop into water (Kennedy 1915, Archilestes). This necessity in the life history ties the winged adults to fresh waters. The males by sex habits remain with the females. Both are adapted in feeding to the numerous minute Diptera and other small flying insects whose larvae live in water or wet soil. Thus the birds which prey on dragonflies must of necessity be associated with fresh water or within dragonfly flight-distance of fresh water.

Poorly developed territorial rights may figure into the picture. In the birds they center roughly about a nesting site surrounded by a food-producing area. In dragonflies the territory is somewhat similarly defined. The female haunts an area pleasing to her as an egg-laying site and as with birds a site surrounded by a food-producing area. The same individual dragonflies will be found patrolling the same pond or stream-pool day after day. In the birds individual territories are sharply fought for and defined. In dragonflies territories are group concerns, more as in colonial birds. In birds territory is defined on physiological factors such as the bird's attachment to the nesting site plus a food producing area. In dragonflies territory is less sharply defined and that on ecological conditions such as local areas suitable for oviposition in a food-producing area. We cite only Nice (1937, 1943) from the literature on territorial rights in birds. The nearest study to the problem in dragonflies is the paper on *Argia moesta* by Borror (1934).

The dragonfly-fresh-water factor narrows the predation problem by the elimination of several extensive groups of birds. All marine or saltwater birds do not prey on Odonata. They are usually fish-eaters. (Our definition of group is physiological and only roughly taxonomic as there are exceptions. One type of exceptions are the birds which occasionally pick up wind-blown dragonflies strayed from a normal habitat). A great group are the birds of plains, prairies and other areas between streams and lakes. Another group is strictly arboreal, while we find a mixed group of birds some of which are too small or too large to be interested in large insects, added to which are a few with special tastes. With 468 named forms of birds in the faunal area (A.O.U. Check List, Ed. IV) 284 forms have no records of having preyed on dragonflies. This leaves 184 bird forms that have records as predators on Odonata. The estimate is involved with at least four disconcerting factors. (1) Dragonflies which have strayed from the fresh-water dragonfly habitat; (2) the practice of many non-insectivorous birds of feeding insects to nestlings and thus probably at such season eating more insects themselves; (3) the weight on economic species; and (4) a less tangible factor that stomachs may not have been collected as ardently in southern horse-fly and chigger areas and in northern black fly and mosquito areas. Under the last the meagre record for southern swamp turkeys showed up first. The last cannot be construed as a criticism as the field problem was vast beyond the efforts of a limited staff. More stomachs in any area were of

more scientific importance than a thinly spread coverage.

Of the 184 bird forms (species, subspecies) which by stomach records had eaten one or more dragonflies per species-record, only 35 birds showed records with 10% of the stomachs per species containing one or more dragonflies each. Sixteen species with less than 20 stomachs examined per species were not counted in the estimate for fear the data were too meagre. But 12 of these had 10% of the stomachs with dragonflies. If we add the two 10% groups we have 47 birds the stomachs of which showed 10 per cent of stomachs with dragonflies. Compared with the total fauna of 468 birds only 47 showed any noticeable predator-pressure in our predator *versus* prey problem. The assumptions in this problem need a word. We took as a minimum twenty stomachs per species because such a small amount of data appeared to be only a general qualitative sample in the known irregular distribution of most bird species. We feel that our figures on 20 stomachs per species as a minimum limit is reasonable and too few stomachs for any final evidence per species. Any mathematical treatment beyond the few preceding becomes very uncertain because we have first to introduce the judgments of the men who supposedly collected at mathematical random and then secondly add our own judgment, to the judgment of the collector without having seen the collector at work. Birds and dragonflies are not planted in rows to be inventoried in checkerboarded plots.

By Elton's (1935) analysis of pyramids of numbers the predator-prey problem in this case is one of the predator (the bird) on the peak of a pyramid of insects, feeding on another predator (the dragonfly) which itself is on a pyramid of smaller insects. That is simple in analysis but on closer inspection becomes deceiving when we examine the predator-prey problem in terms of possible and probable contacts between the two. The probability of necessary contact between the two fades out to where Darwinian survival probably favors the prey. (Gabrielson 1941).

For the predator to exterminate or even to reduce the prey the predation has to be continuous enough to keep up a continuous attrition or depletion of the numbers of the prey. Our evidence shows no bird species attacking dragonflies exclusively, an ideal pyramid peak, if found. One approach to the predator-prey problem is by way of the pyramid of numbers concept which we will examine as applied to the specific bird-dragonfly problem. We find at once several factors which involve the specific bird-dragonfly problem. (1) Nearly all the birds involved north of Mexico are migratory. The dragonflies are attacked by northern birds in the winter and by southern birds in the summer. This is a pyramid peak shift. (2) Many small birds during the breeding season feed their young on insects though they may be seed-eaters at other times and not then interested in dragonflies. This food shift reduces the usefulness of the pyramid concept as a unit of ecological analysis. (3) A third difficulty arises in the triple life of the dragonfly prey, as eggs and nymphs in a water environment the year around but in warm months as adults in an aerial environment. These involvements raise the problem to three very outstanding variables with each of which are innumerable minor variables. Thus the symbol of a stable triangular pyramid hardly diagrams a system of three cycles, (1) the migratory shift; (2) the food shift; and (3) the dragonfly shift from water to air. Its basic instability for a precisely drawn pyramid makes the pyramid deceptive. It reminds one of the astronomer's simple problem of three bodies moving freely in space, a problem as yet with no exact formula for the position of the Moon at any moment in relation to the Earth and Sun. The human mind craves constants but in biology deals with variables. (Errington 1946).

We have no certain suggestion for a diagram to clear this impasse for even the one problem of birds *versus* dragonflies. We have come to believe that, if a usable symbolic diagram is finally discovered it will have to be cyclic and may be found in the field of cycloid systems in spherical geometry, certainly not in plane geometry. Then develop the diagram to the hundred species of insects one species of bird may eat! Then follow the bird on a summer of hard work in the Subarctic and on a winter vacation to South America. The pyramid of numbers symbol is useful but has a deceptive appearance of stability. By label and theoretical structure it is composed of predators and prey. In reality it is functional and composed of cyclic functions. In the experienced hands of Elton as conceived for pure aggregates of fish-eating birds the pyramid of numbers is a useful concept. For other complexes of predator and prey it has to be used with discretion. Elton himself used it so.

This complex of two types of predators each operating in patterns of two or more seasonal behaviors which could puzzle good mathematicians has just been stated in its basic elements. We despair of breaking it down into the level of pyramids of numbers used by Elton (1935). The deadly evidence from examination of stomach contents, beyond which there is no rebuttal evidence, shows pyramids so scrambled in factors of time and material that it becomes exceedingly difficult to use pyramid concepts and symbols in its analysis. As shown by McAtee, Henderson and the Biological Survey's own data the bird at the peak of its usual pyramid slips down to lesser peaks when actually hungry on the greater peak. The pyramid concept is useful this far.

We do not wish to disparage ecology. Gradually that science is accumulating good diagrams and symbols and is slowly shifting from a descriptive form to one of energies and energy relationships.

More and more we have visualized the problem of bird *versus* dragonfly as one that swings around the contact of bird and dragonfly. The contact between predator and prey is the critical point in space and time for both elements, the bird and the dragonfly.

In a general system of energies a transfer of energy (dragonfly to bird) takes place at the point of contact. At the same general time and place a change of energy takes place (dragonfly energies into bird energies).

The contact is fairly stable in locality as far as the prey is concerned. In our case of bird *versus* dragonfly, the predator occupies a very unstable position in the matter of contact. Except at brief aggregation for migration (see Tavener 1935 on migratory aggregation and this article "Pigeon hawk (*Falco columbarins*)" the bird predator cannot attack the prey *en masse*).

(1) During breeding season bird families are separated and scattered by territorial rights except for some species which recognize common feeding areas. By the desire for privacy during the breeding season birds are more thinly scattered than at other times. This tends to draw stream and marsh loving birds away from the usually narrow shore and stream habitats of the dragonfly prey.

(2) Colonial birds tend to nest in small densely populated areas which, if dragonfly eaters, have colonies so widely scattered the bird predator tends to leave areas unattacked in between colonies. This is true of the yellow-headed blackbird in western tulle marshes, of martins limited to man-made bird houses and probably of the colonies of Franklin gulls in the north.

(3) The usual scattering is by ecological discontinuities. Dragonflies are very attached, each species, to a particular type of bottom, of density of vegetation, speed of water-flow and maximum and minimum temperatures. On the same lake system Ophiogomphus lives on sand bottom abundantly studded with cobble stones, Gomphus on mud bottom while Progomphus is usually limited to pure sand bottom in moving but not rough waters. (Straits of Macinac, Burt and Douglas Lakes, Mich.) These choices by the female while ovipositing are probably made by the female on surface characters of the water, wind drifts, and emergent and riparian vegetation. She does not examine the bottom and probably has no memory of it from nymphal days. But it gives a very local and discontinuous distribution of each species of dragonfly. If attacked by fly-catchers each species of which has a preferred type of outlook branch or limb, such choice outlooks may be so scarce that whole areas of proper dragonfly bottom may have no covering fly-catcher. The breeding waterfowl of the Canadian lakes and streams are equally particular about the type of shore-vegetation cover they choose for their nests and young brood. Food is abundant and secondary to protection for the predator in a competitive field. Our answer for the survival of dragonflies in a world of predator birds lies in the complexities of microecology. The bird predator cannot be particular about its home and its location and at the same time harvest the crop of dragonfly-prey. Contacts of predator-bird and prey-dragonfly become disjointed in space and time. The contact is the basic essential in Darwinian survival. In our present minor problem it does not operate to finality.

Another general factor enters the problem of survival of the prey-dragonfly. To survive down through evolutionary time the predator is usually a species that has to some extent food tastes broader than such as would make it obligate to dragonflies. Such tastes in the types of birds which do use dragonflies usually spread out beyond that for dragonflies to other insects which could be classed with Odonata physiologically rather than taxonomically. All bottom nymphs are food for those feeding on odonate nymphs. Many species of flying insects are common food for birds which eat adult Odonata. In the aquatic birds food tastes spread even farther into crustacea, fish, molluscs. In the flying birds the raptores may use mammals and other birds. This relationship of predator to prey is just the opposite of that of an obligate parasite to its one host.

This outside field of food other than that of Odonata makes for a plastic relationship between predator-bird and prey-dragonfly. It saves the bird at any scarcity of dragonflies and saves the dragonflies by the greater number of smaller insects drawing the fire of the predator-bird. (We badly need a physico-mathematical treatment of relative size in the predator-prey relationship and with it the same study of the parasite-host problem of relative size.)

We have written enough to give our general impressions (conclusions?) while sorting the great mass of data assembled by the experts of the U. S. Biological Survey to say that there is little evidence that any species of North American bird stands much of a chance of exterminating any species of North American dragonfly. The two faunas will wing their way together down through evolutionary time. Many contacts of predator-bird with prey-dragonfly will be made but none critical by species-healthy birds on species-healthy dragonflies.

Less than a half dozen species of birds appear to have a keen interest in dragonflies, the Franklin gull, the lesser yellow legs, the purple martin, the yellow-headed blackbird, the belted kingfisher and two marsh wrens. Except the lesser yellow legs on which we have no nesting data all use dragonflies heavily to feed nestlings.

We have come to believe that in the evolution of dragonflies down through the ages continental or even world changes in climate are at least partially responsible for the geological succession of dragonfly faunas. Coupled with this is the accumulating evidence that succeeding new species are produced by the several types of chromosome and gene change with what the geneticists term gene flow in populations. Dragonflies live in a keenly competitive world but for some illy defined reasons have a wide margin for survival.

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VEGETATION OF THE WEQUETEQUOCK-PAWCATUCK TIDAL-MARSHES, CONNECTICUT

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VEGETATION OF THE WEQUETEQUOCK-PAWCATUCK TIDAL-MARSHES, CONNECTICUT

INTRODUCTION

The purpose of this report on the saline tidal-marshes[1] between the Wequetequock[2] and Pawcatuck[3] Rivers, New London County, Connecticut is twofold: *1*, specifically, to describe the local natural and semi-natural vegetation of ferns and seedplants, its segregation into communities, their structure, floristic composition and inferred correlations with environmental factors; and *2*, generally, to describe that vegetation in a form suitable for general use, and thus to contribute to our basic knowledge of Atlantic coast (Fig. 1) and of Connecticut tidal-marshes (Fig. 2), particularly in regard to the orderly segregation of communities in respect to surface slope, to undrained depressions and islands, and to effects of estuaries ditching and mowing. Fire and grazing, though not now occurring, may have been active in the past, with effects continuing into the present. No detailed environmental analyses are here reported, nor are the extremely interesting algal components of the vegetation discussed. The construction of dikes, the flooding of large areas of marsh with brackish water, and the creation of habitats suitable for wildlife are the chief activities in the state-owned areas: reports on resulting vegetational changes may appear in the future. No attempt is made to review critically the scattered tidal-marsh literature, or to repeat the information of that literature.

The data here presented were obtained in conjunction with the wildlife research being carried out on lands owned and administered by the Connecticut State Board of Fisheries and Game. Grateful acknowledgment is made to that Board for their very complete cooperation and willing assistance, particularly to Dr. R. P. Hunter, Superintendent of the Board, to A. L. Lamson, Game Management Supervisor, and to L. A. Williamson, Game Management Technician, who has drawn all the figures for this publication (except Figs. 3 and 5). Fig. 3 was prepared by W. Thayer Chase of the Connecticut State Park and Forest Commission. The photos are the property of the Board of Fisheries and Game, and were taken by J. Seaylea on August 25, 1947, except for Fig. 14b, taken by D. Deane on October 4, 1948. The senior author spent the entire summers of 1946 and 1947 in residence on the area, under a State Board Fellowship for graduate study in the Department of Forestry and Wildlife Management at the University of Connecticut. This paper is adapted in part from a thesis for the degree of M.S. in that University (Miller 1948). The junior author spent 21 days on the area in 1947, from May through September, and about an equal period in 1948.

The authors wish to express their sincere appreciation to Miss Leta Hughey of the U. S. Forest Service, who has contributed the plate on the vegetative characteristics of tidal-marsh grasses (Fig. 5). These drawings are based on materials collected by the authors from the area, except for: *Festuca rubra,* from Forest Service sheet 76,677, Utah; and *Hierochloë odorata,* Forest Service sheet 18,942, Utah. Acknowledgment is also made to Dr. H. P. Brown, New York State College of Forestry, Syracuse, for identification of the upland tree wood found in situ in the marsh. The Latin nomenclature of the plant species is that of Gray's Manual, 7th edition, except for that of the grasses, which follows Hitchcock's Manual, 1935. Identification of temporary plant collections was made at the herbaria of Connecticut College, University of Connecticut and Yale University. A thorough systematic survey of the seedplants, involving complete collections, was planned for the 1947 season but has been temporarily postponed.

The authors gratefully acknowledge the valuable criticisms on the manuscript of this paper made by Prof. G. S. Torrey, University of Connecticut.

It is to be deplored and regretted that not a single area of virgin unmodified or preserved tidal-marsh exists in Connecticut for purposes of comparative study and research. Any such "natural area" would have extraordinarily high value in all programs of basic research on marsh problems. not only in the plant sciences, but in regard to wildlife and to mosquito studies as well. Existing marshes have been lacerated with ditches with that admirable thoroughness and pseudo-foresightedness with which mankind is apt to treat the lands of his heritage. In this instance, the advent of modern methods of insect control calls into critical question the present necessity of such ditching, at best a violent activity which, though it destroys the mosquitoes, also destroys the permanent pools so valuable to wildlife, completely rearranges the mosaic of natural plant communities, and eventually produces other pools of the same kind that the ditches were designed to eliminate. Until a suitable area of preserved tidal-marsh becomes available for unbiased research and is allowed

[1] The term "saline tidal-marsh" or more simply "tidal-marsh," is used rather than "salt marsh," as being more definitive of the actual conditions. Tidal marsh thus includes all coastal marsh under tidal influences, almost all of which is saline. "Salt marsh" is considered a wider, more inclusive term, embracing all marsh under saline influences, both coastal and interior.

[2] Pronounced Wee'-ke-tee-kwak.

[3] Pronounced Paw'-ka-tuck.

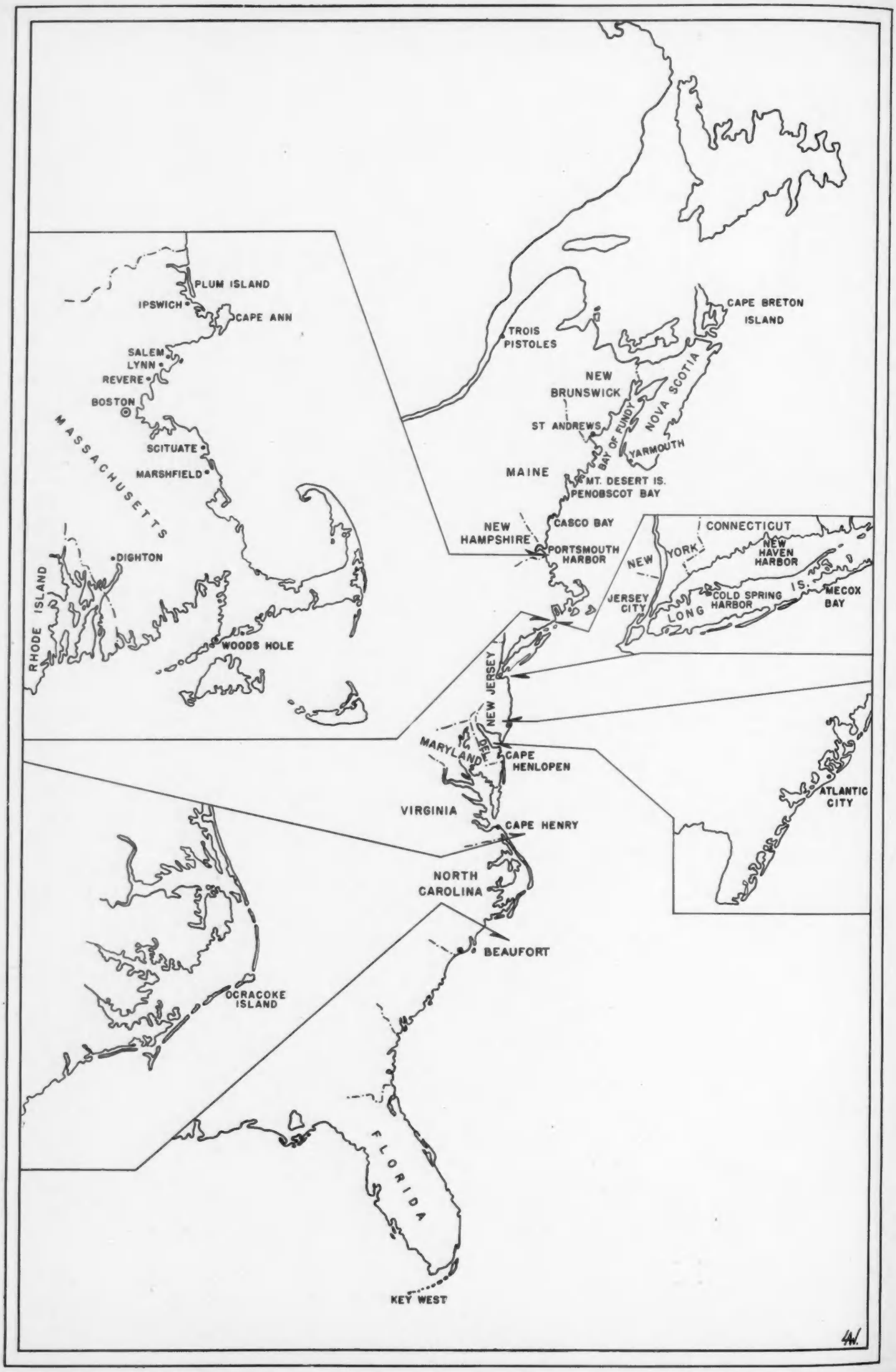


FIG. 1. Map of the Atlantic coast of North America, showing the localities at which tidal-marshes have been described.

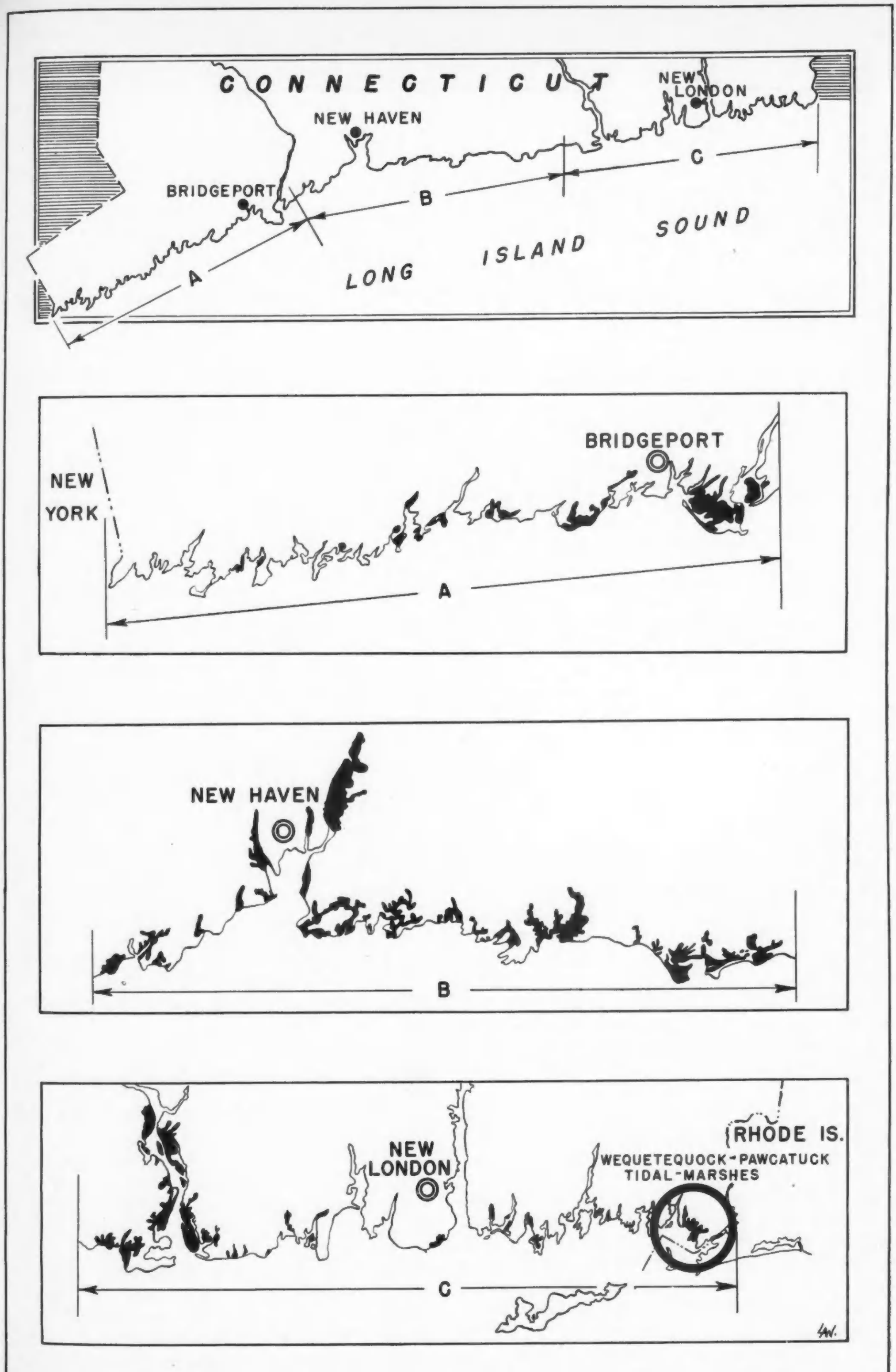


FIG. 2. Maps of the Connecticut coast, showing the more important areas of tidal-marsh. Top, key map. A, western section. B, central section. C, eastern section; Wequetequock-Pawcatuck area encircled. Data mainly from Flint, 1930.

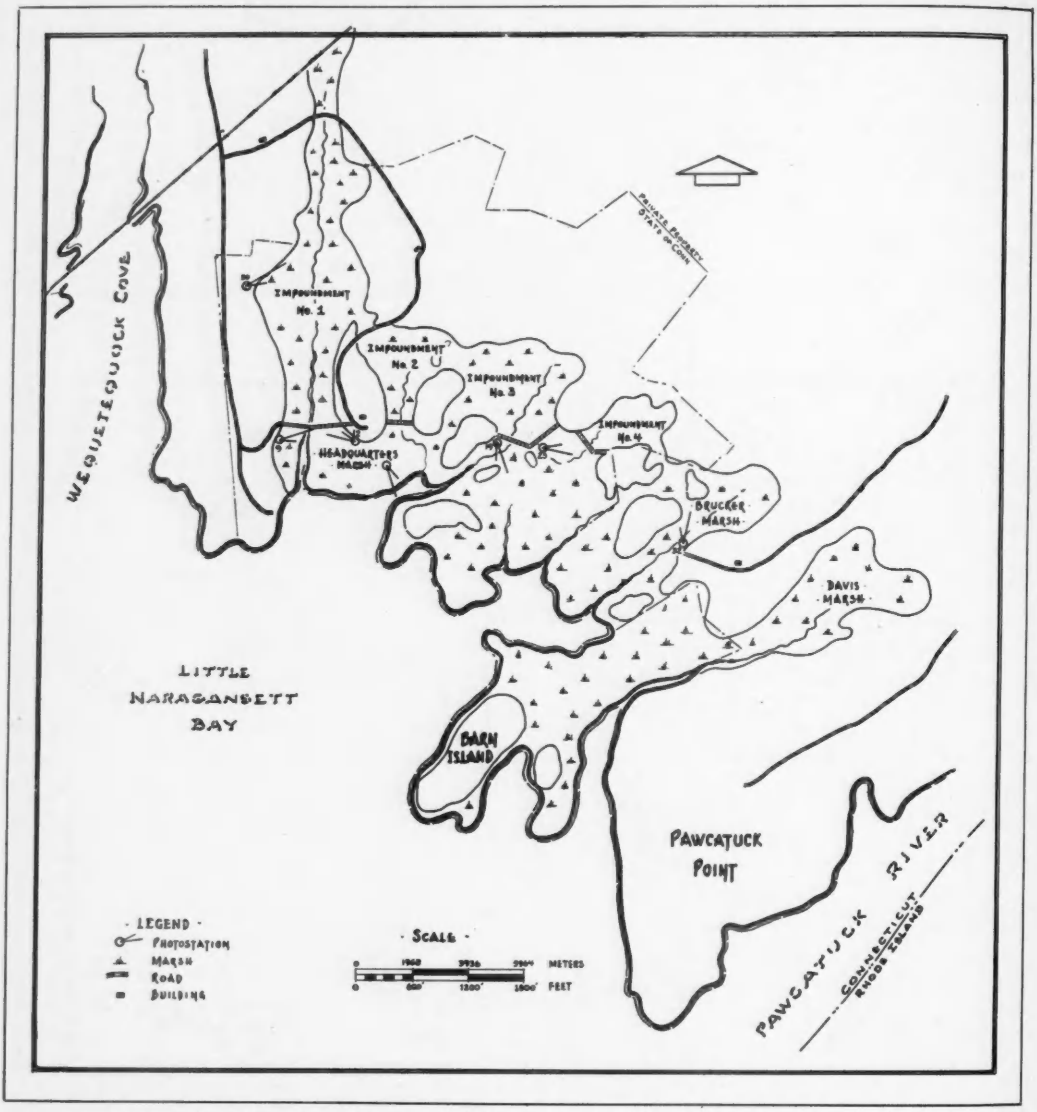


FIG. 3. Map of the Wequetequock-Pawcatuck tidal-marshes, showing localities mentioned in this study. Control from Fairchild Aerial Survey Negatives. The area lies wholly in Stonington township, New London County, Connecticut.

to revert to a natural equilibrium, many important problems must remain unsolved.

THE AREA AND ITS LOCATION

The area of marsh here referred to as the Wequetequock-Pawcatuck tidal-marsh is a single compact unit of about 1.4 sq. km (.52 sq. miles), in New London County, lying close to the Rhode Island border (Fig. 3). The marshes occupy a protected area bounded on the west by a headland at the mouth of Wequetequock Cove, on the east by a headland at the mouth of the Pawcatuck River, and on the south by Little Narragansett Bay, which bay is separated from Long Island Sound by bars and islands extending west from the Rhode Island mainland.

The marsh is not only continuous between the headlands of the two rivers, but it extends up as finger-like projections into six minor valleys, of which the westernmost one is considerably larger than the other five.

This form, with its uniform bay-front marsh, and its six essentially similar "valley-marshes," makes the region ideally suited for a research program involving different treatments for each of the valleys. In these respects, the area is unsurpassed by any other marsh on the coast of Connecticut.

Over 160 hectares (400 acres) of marsh and adjacent woodland, comprising the four western fingerlike projections, are owned by the State Board of Fisheries and Game, and designated the Barn Island Game Management Area. This area is being developed through management and research in connection with the control of waterfowl populations. Four dikes have been constructed, creating four impoundments of brackish water (Fig. 3) that should supply additional feeding grounds for many types of waterfowl, chiefly ducks.

THE TIDAL-MARSH AS A LAND-FORM

The tidal-marsh of the New England coast is a distinctive and easily recognized land-form. It is a flat meadow at or below the level of the highest tides, originally bounded abruptly on the landward side by scrubby and forested uplands and by freshwater swamp and marsh, and equally abruptly on the seaward side either by a bay-mouth sandbar, or by an escarpment of 0.5-1.0 meters leading to a muddy tidal flat. The marsh substratum is generally a fibrous peat, mixed with more or less silt or sand, and is considered to be mainly an organic accumulation in valley mouths and behind off-shore bars. Johnson (1925) has adequately summarized our knowledge of the New England type of tidal-marsh.

This tidal-marsh is a geologic land-form developing in conjunction with a shoreline of post-glacial progressive submergence. Such a shoreline is not to be confused with those following emergence, or following a single isolated submergence. The stages associated with progressive submergence are well portrayed by Knight (1934) for the New Haven (Connecticut) region. His stages (Fig. 4) are outlined below:

A. During early submergence, a bay-mouth bar develops between two headlands, formed of detritus from those headlands. A sheltered lagoon forms behind the bar.

B. Submergence continues and a part of the bordering upland and freshwater swamp is destroyed. The lagoon fills with silt to a certain level; then builds up with *Spartina alterniflora* (= *S. stricta*); then builds up to a hightide level with *Spartina patens*. (The so-called Shaler Marsh.) The bar moves landward.

C. Submergence continues and more of the upland and freshwater swamp are destroyed by encroaching tidal-marsh. The lower silt and Spartina-alterniflora-peat[4] horizon remains unchanged; Spartina-patens-peat layer thickens. Bar moves landward.

D. Submergence continues and more of the upland and freshwater swamp are destroyed. The Spartina-patens layer becomes thicker. The bar moves farther inland.

E. Submergence continues and more of the upland and freshwater swamp are destroyed. The patens

[4] Following the practice of certain fields of electrical engineering, hyphens are used to connect words which collectively serve as one term, at times when the meaning might otherwise be obscured. Thus, "Big Cypress-Swamp" and "Big-Cypress Swamp," as used in Florida, are two different terms.

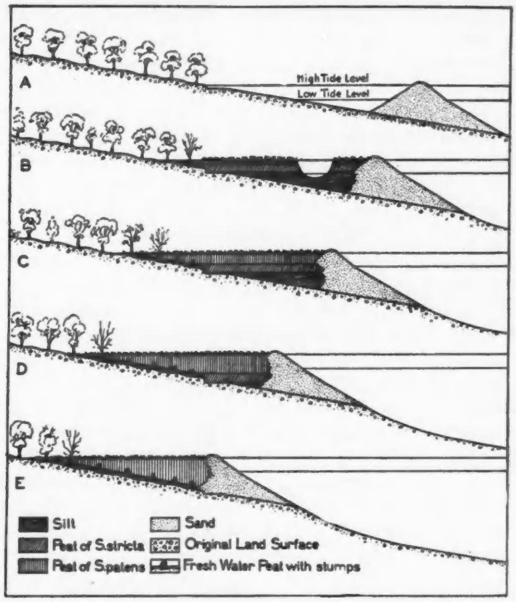


FIG. 4. Diagram to illustrate five stages, A through E, in the theoretical constructional history of a typical New England tidal-marsh. (After Knight, 1934.) The significance of these geologic data has been oddly overlooked by plant ecologists, who have repeatedly hypothesized a plant succession culminating in a relatively high and dry *Juncus gerardi* marsh, and even an upland forest. Strangely, under the influence of normal shoreline development and a progressive submergence of the land, and most noticeably when the marsh fronts directly on the bay, the actual vegetational development would be excellently exemplified by the succession diagrams already published—if the arrows were all reversed!

layer becomes thicker. The bar moves so far inland that it now overlies freshwater-peat and upland remains at the bottom of the marsh; no silt or alterniflora layers remain. (The so-called Mudge-Davis Marsh.)

F. The original bar is completely removed by erosion leaving the tidal-marsh unprotected and itself exposed to erosion. The eroded front is composed of patens peat, overlying freshwater peat and upland remains. The Wequetequock-Pawcatuck marshes are believed to exemplify this stage. Small secondary bars may develop locally, superimposed on the peat front.

It is not agreed as to whether the progressive submergence is continuing to the present day. Both empirical data and the interpretation of them are conflicting. At least in some local cases an apparent subsidence may be entirely fictitious, and may be due instead to an increase in the effective high-tide level, as caused by changes in nearby bars and land masses (Goldthwait 1936a, 1936b, Johnson, D. W. 1910). On the other hand, actual tidal data for the entire Atlantic coast (Marmer 1948) do indicate a small but consistent rise in sea level, based on measurements some of which date from 1893. Apparent recent changes of sea level occur on the Barn Island

Area, as evidenced by buried stumps and by invaded freshwater marsh. Several buried stumps are reported, and one in situ stump is here recorded under about 30 cm. of peat, identified as a white oak by H. P. Brown of the New York State College of Forestry. Characteristics of the supposedly invaded freshwater marsh are described in the section on the Patens Lower Slope as a "Peat-hummock Type" (p. 159).

BOTANICAL LITERATURE

Our knowledge of the local tidal-marsh vegetation of the North American Atlantic coast is still sketchy and irregular (Fig. 1). In the absence of any recently published review, the following survey is appended as a contribution to the bibliographic knowledge of this region. The geologic literature is included only when it contains specific data on the past or present plant communities. The several localities specifically described by Johnson (1925) in his geologic study are not included. Chapman's (1940b) paper on the New England marshes is mainly a compilation of succession diagrams as interpreted from the literature. Uphof's (1941) comprehensive world review of the halophyte problem includes a bibliography of 363 titles.

QUEBEC. Prat (1933). Descriptive study of vegetation of rocky shores and tidal-marshes. Trois-Pistoles.

NEW BRUNSWICK. Ganong (1903). Monographic study of natural and diked marshes. Head of the Bay of Fundy, partly in Nova Scotia.

Klugh (1909). Laboratory experimentation, following field observations on the excretion of NaCl by *Spartina alterniflora*. St. Andrews.

NOVA SCOTIA. Dawson (1855). An early report on buried-in-situ pine and beech. Head of the Bay of Fundy.

Transeau (1909). Includes a 1-page description of the local marshes. Yarmouth.

Nichols (1918). Includes a 7-page discussion of salt and brackish marshes. Northern Cape Breton island.

MAINE. Kemp (1862). Descriptive account of six zones, from beach to deep sea; primarily algae. Peak's Island, Casco Bay.

Penhallow (1907). General discussion of marsh development from Cape Ann (Mass.) to Casco Bay (Me.). Detailed history of a marsh based on soil and peat horizons; Portsmouth Harbor.

Hill (1923). Includes an 8-page description of the local marshes. Penobscot Bay.

NEW HAMPSHIRE. Davis, C. A. (1895). Descriptive comments on interesting species, with vegetational notes. Portsmouth Harbor.

MASSACHUSETTS. Mudge (1862). Discussion of marsh history based on buried-in-situ cedars. Lynn.

Shaler (1885). General physiographic treatment; minor botanical comments; catalogue of larger tidal-marshes between Hudson River and Casco Bay (Me.). Detailed account of Plum Island marshes near Newburyport; and of Green Harbor River diked lands at Marshfield.

Rich (1902). Includes comments on marsh plants. Oak Island, near Revere, north of Boston.

Kearney (1904). Studies of salt content of marsh soils. Woods Hole.

Bartlett (1909). Descriptive account, with plant lists, of zones from tidal-marsh to Chamaecyparis bog. Woods Hole.

Davis, C. A. (1910). Peat studies of vertical sections of marshes. Boston.

Johnson, D. W. (1910). Effects of storm in breaking through a bar, and raising the high-tide level of the lagoon behind. Scituate.

Davis, B. M. (1913). Includes description of algal communities of marsh pools. Woods Hole.

Townsend, C. W. (1913; 2 ed. 1925). A naturalist's account, including several chapters on tidal-marshes. Ipswich.

Wherry, E. T. (1920). Acidity studies of different tidal-marsh communities. Oak Island, near Revere, north of Boston.

Goldthwait, J. W. (1936a). Evidence against recent change of sea levels, based on remeasurements of marsh lands. Ipswich.

Goldthwait (1936b). Evidence against recent change of sea levels, based on tide levels on rock ledges. Salem.

Chapman (1940a). A monographic treatment; environmental analyses. Romney Marsh, west of Lynn.

Dexter, R. W. (1947). A monographic study, including a description of the *Spartina alterniflora* and *S. patens* communities. Cape Ann.

Johnson, F., and H. M. Raup (1947). Includes vegetation studies, and analyses of peat sections. Grassy Island, near Dighton.

CONNECTICUT. Nichols (1920). Devotes almost one third of the paper to salt and brackish marshes. General for the state.

Steiner (1934). A monographic study on cell-sap and soil analyses, and osmotic values. New Haven Harbor.

Steiner (1935). A general description of the vegetation, based at least in part on the author's local studies.

Knight (1934). A geologic study of tidal-marsh history, showing a genesis combining the Shaler and the Mudge-Davis theories. East of New Haven Harbor.

NEW YORK. Transeau (1913). Includes 3-page descriptive account of marshes. Cold Spring Harbor.

Johnson & York (1915). A monographic account of local conditions. Cold Spring Harbor.

Conard (1924). Resurvey of certain quadrats described in Johnson & York 1915, after 12 years. Cold Spring Harbor.

Conard & Galligar (1929). Resurvey of same quadrats, after 6 more years, showing invasion by freshwater marsh. Cold Spring Harbor.

Conard (1935). Includes 8 pages on tidal-marshes. Central Long Island.

Taylor (1938). Monographic study of vegetation and environment of marshes. Various localities in Long Island.

Taylor (1939). Observations and experiments on tidal-marsh plants in relatively fresh water. Mecox Bay, near Bridgehampton, Long Island.

NEW JERSEY. Harshberger (1900). Includes 4-page descriptive account of marshes. Near Atlantic City.

Harshberger (1902). Miscellaneous notes, including some on marshes. Eight localities.

Smith (1907). Mainly management and economics. With map showing salt marsh areas for entire state.

Harshberger (1909). Includes comments on marshes. Northern coastal New Jersey.

Harshberger (1911). Salinity studies of marsh soils at various depths. Northern coastal New Jersey.

Harshberger (1916). Origin and development of marsh pannes. Non-regional, though presumably based on New Jersey experience.

Harshberger & Burns (1919). Includes 1-page account of tidal marshes. Near Jersey City.

DELAWARE. Snow (1902). With comments on a brackish marsh. From Cape Henlopen south for seven miles.

Snow (1913). With comments on certain marsh plants. Same area.

MARYLAND. Shreve *et al.* (1910). Includes 3, 1, and 10 pages respectively on the tidal-marsh flora, western-

shore marsh vegetation, and eastern-shore marsh vegetation.

VIRGINIA. Kearney (1901). Includes 7 pages on marsh vegetation. South-eastern Virginia.

Egler (1942a). Includes 1 page on local tidal-marsh vegetation, and annotations on tidal-marsh species. Seashore State Park, at Cape Henry.

NORTH CAROLINA. Kearney (1900). Includes 3 pages on tidal-marsh vegetation. Ocracoke Island.

Wells (1928). With a half page on the tidal-marshes of the state.

Reed (1947). Soil analyses at four stations of the Spartina glabra community and of adjacent communities. Beaufort.

FLORIDA. Harshberger (1914). Includes two pages on tidal-marsh vegetation. General for the state.

Davis (1940). Includes two pages, with a plant list, on tidal-marsh vegetation, and its distribution among the mangroves. General for southern Florida.

Davis (1942). Includes short discussion of a small tidal-marsh. Boca Grande Key, west of Key West.

Davis (1943). Includes two pages on tidal-marsh vegetation. General for southern Florida.

THE TIDAL-MARSH AS A VEGETATION HABITAT

Tidal-marshes in general and those of southeastern Connecticut in particular possess certain very distinctive ecologic conditions. These have been variably studied and discussed in the literature. The earlier publications in part were very quick to analyze this saline environment and to draw cause-and-effect relationships between the salinity and the vegetation. A more mature ecologic philosophy, together with certain unexpected results from analyses of that environment, demands greater caution. It seems wise at present to utilize our knowledge only for drawing correlations, but not otherwise. No detailed environmental analyses are here reported, although certain new interpretations are adopted. The more outstanding ecologic conditions are as follows:

1. Tides. Tidal influences are probably the most obviously significant environmental factors which appear to be responsible for the segregation of this type of vegetation. Of these influences, tide levels have been well investigated (Johnson & York 1915). The marginal strip of *Spartina alterniflora* is subjected to regular floodings by saline bay waters twice a day. The general extent of the marsh is flooded less often, and may be flooded completely only during the highest tides of spring and fall. The high upland margin of *Panicum virgatum* is flooded only exceptionally.

2. Salinity. The shoot systems of the plants are submerged in saline bay water at every flooding. The root systems are in saline solutions of varying concentrations, often less than those of the flooded shoots. Subsoil seepage of fresh water from the uplands may create a brackish environment in what would otherwise be an area of high salinity due to surface tidal flows. Taylor's (1939) studies indicate that many marsh species grow more luxuriantly in the less saline situation, and imply that their abundance in the marshes is an example of an "emergence into dominance" where relieved of the competition of other species.

Extreme salinities are to be found on certain occasions in the pannes. These extremes are believed from the present study to be very important in altering the vegetation at such times, with effects that persist for many years after.

3. Water Tables. The water table below the unflooded marsh, according to Taylor (1938) fluctuates only slightly. Its salinity fluctuates scarcely at all, and its level varies from 5-40 cm. below the surface.

The present authors believe that some marshes must show additional complications. For example, during high flooding tides on the Wequetequock-Pawcatuck marshes, some of the surfaces, normally firm, become springy and even quaking. This situation implies that a firm surface stratum of peat rises by entry of tide waters below it, which waters in turn must affect the salinity of the ground water.

4. The Soil. The inorganic substratum below the marsh is the sandy till of the regional ground moraine. This till appears at the surface on the various islands within the marsh, and on the adjacent upland. Frequently, a 5-10 cm. layer of hard clayey sand is interspersed between the till and the marsh peat, the origin of which was not investigated. This layer was analyzed by the Bouyoucos (1930) method and found to contain an average of 64 percent sand, 22 percent silt and 14 percent clay. Comparable analysis of a single sample from a nearby upland showed 43 percent sand, 48 percent silt and 9 percent clay, indicating a marked increase in the proportion of sand for the layer below the marsh.

The marsh peat was investigated in a series of soil samples. In general, the uppermost 15-30 cm. is a hard and firm layer and consists of undecayed plant fragments mixed with sands. The amount of sand varies locally from 0-50 percent. It is this layer which frequently rises when flooded by tides. Below this horizon the peat is relatively decomposed and becomes soupy during high water levels.

The acidity of the marsh soil has been but rarely studied. Wherry (1920) obtained the interesting data that the marsh itself is moderately alkaline, the Panicum virgatum Upper Border strongly acid, and the general upland slightly acid. The striking individuality of the Upper Border is in line with its floristic and vegetational individuality.

5. Mowing. Mowing has not been considered a significant vegetational factor in the previous literature of Atlantic coast marshes. There is strong local evidence that prolonged mowing of the highest zones reduces the vitality of the predominant species apparently causing the increase of Triglochin (poisonous to stock), eventually bares the soil, and is followed by soil erosion. Mowing on some marshes has apparently occurred continuously since colonial times, and has undoubtedly affected the nature of the vegetation. Details are discussed in a later section.

6. Mosquito-ditching. Taylor (1938), working throughout Long Island, reached a final conclusion which applies "only to the area studied," that "ditching has made no fundamental change in the makeup

of the salt marsh vegetation." The authors are not fully in accord with this point of view. For all areas known to the authors, not excluding Long Island, ditching has drained the pools which probably once supported a higher wildlife population, and has thus initiated a long succession of vegetational changes. Conspicuous marginal effects are related to (a) the turf-line (the line of turf left beside the ditch when it is excavated), (b) the bare sides of the ditch, and (c) natural levees which develop on each side of the ditch. These natural levees markedly alter the surface drainage conditions of the entire marsh, and sometimes tend to produce elongate pannes and pools in the inter-ditch areas that are conspicuous at some seasons.

In some parts of the area the turf-line was originally laid up so uniformly and continuously along one side of the ditch that at present it forms a small though very effective dike. Such a turf-line effectively retards drainage from the very sites that the ditch was intended to drain.

7. Surface-level Changes. From the present studies, the authors infer that surface-level changes are in active progress in the marsh. These changes are related to at least four processes: (a) normal up-building of the peat level, possibly in correlation with the rise in sea-level; (b) soil erosion, assumed to result locally from excessive mowing; (c) deposition, as that known to occur on natural levees along ditches and estuaries; and (d) compaction of the marsh peat, a phenomenon known to occur in bogs, and assumed to occur in the marshes. It is suggested that compaction may be correlated with numerous circular depressions apparently not connected with any surficial action.

8. Precipitation and Temperature. The nearest Weather Bureau station is at New London, ten miles west, and the following data were obtained from Kirk (1939). The local climate is that typical of much of New England, moderated in part by its proximity to the ocean. The average length of the growing season, based on records of 48 years, is from April 14 to October 27, a total of 196 days. Average monthly temperatures in degrees Fahrenheit, based on 65 years, are as follows for January to December respectively: 29.5, 29.1, 37.0, 46.7, 57.3, 66.1, 71.5, 70.0, 64.1, 53.8, 43.0, and 32.7.

Average monthly precipitation in inches, based on 65 years, are as follows for January to December respectively: 4.12, 3.77, 4.16, 3.74, 3.50, 3.24, 3.68, 4.28, 3.48, 3.73, 3.72, 3.62, with a total annual precipitation of 45.04. Average monthly snowfalls in inches, based on 47 years, are as follows for the months of October to April respectively: 0.1, 1.6, 5.8, 9.4, 10.7, 5.1, and 1.0, with a total annual snowfall of 33.7 inches.

9. Hurricanes. The severe tropical disturbance of 1938 has been a forcible reminder that destructive wind storms, though often local in their damage, occur repeatedly in Connecticut. About twenty have been recorded since 1786. Any marked effect of such storms on the herbaceous marshes themselves is not readily apparent. Destructive effects are limited to physical breakage in adjacent forests, killing by salt spray and by salt water inundation, and blanketing by hurricane debris. The 1938 hurricane littered the Panicum virgatum Border and adjacent upland with constructional timbers, often intact sides of houses, from the summer homes on the bar across Little Narragansett Bay. In addition, the red maple swamps at the heads of the valley-marshes appear to have suffered considerably by breakage and saline inundation. As is so often true of natural vegetation, these plant communities will be in process of recovery from this disturbance for many years, and will probably not have fully recovered before the next hurricane, since the age of overmature trees is greater than the average interval between hurricanes.

10. Fire and Grazing. These factors are undoubtedly important elsewhere in the tidal-marshes. Locally, however, neither fire nor grazing has occurred significantly in recent times. The role of Indian fires in pre-colonial days, however, is discussed elsewhere.

In conclusion, it is well to consider that the ecologic factors of the tidal-marsh may be grouped as (1) constant continuously acting factors, such as normal tidal changes, and (2) abnormal extreme factors, such as evaporation to dryness of the saline waters of a panne. These extreme factors—so frequently overlooked in ecologic studies—cannot be neglected in interpreting the existing vegetation, although their importance must at first be a matter of interpretation rather than experimentation.

It is not to be overlooked that the tidal-marsh ecos[5] acts as a single integrated phenomenon. Although we may correlate certain ecic factors with certain vegetational characteristics, it is premature to affirm dogmatically any cause-and-effect relationship, despite the fact that this has been done in the past.

HISTORY OF THE AREA

The history of the tidal-marshes is varied and complicated. Contrary to early twentieth century ecologic philosophy, the authors do not assume that its history can be suitably described in terms of a single virgin untouched climax, which the hand of man has since defiled and destroyed. It appears more reasonable to consider the marsh as having been in adjustment with geomorphic processes and with surrounding human populations almost since its inception. This vegetation development is still continuing.

1. Geologic Origins. The geologic stages in the development have been discussed earlier in this paper. Man appeared on the scene probably sometime during stages B or C (p. 149) and thereafter his effects accompany the rise and landward shift of the marsh.

2. The Indian Period. An interpretation of the vegetation of the period rests largely on an interpre-

[5] *Ecos*, the biologic environment considered as a whole, or a system, existing at a certain level of integration. *Ecic* is the corresponding adjective. For related discussions of this holistic concept, see Cain (1944: 16) Egler (1944b) and Redfield (1942).

tation of the role of fire, since kitchen middens and camp sites have not been recognized on the Wequetequock-Pawcatuck marshes. Indian populations, however, are known to have occurred in the vicinity, and artifacts have been found in nearby fields. Following the opinion of Bromley (1935) on the significance of Indian fires, it is suggested that these marshes were burned over, either accidentally or purposely at fairly frequent intervals. The effects of fire on marsh vegetation, particularly on the shrubby Iva, are unknown at present.

3. The Colonial Period. The period was characterized by a relatively rural population of Europeans. The effect on the marshes was largely one of mowing, as salt-marsh hay was extensively used for bedding, packing and mulching. The removal of such grass from the land not only reduced the fire hazard, but would have restricted the development of Iva if it were tending to invade.

4. The Pre-Ditching Period. During the 19th and early 20th centuries there was a gradual change in land utilization of the marshes and surrounding up-

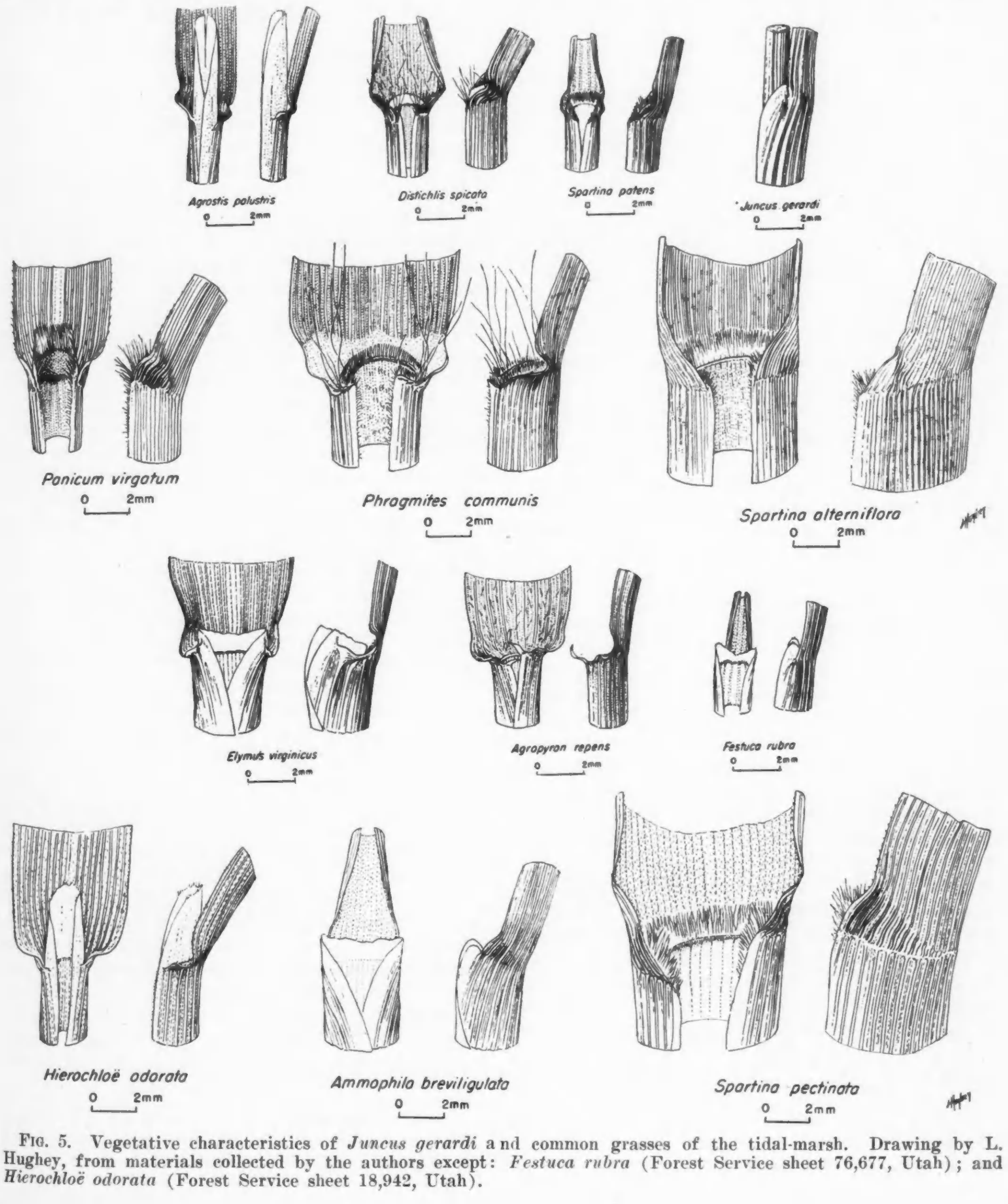


FIG. 5. Vegetative characteristics of *Juncus gerardi* and common grasses of the tidal-marsh. Drawing by L. Hughey, from materials collected by the authors except: *Festuca rubra* (Forest Service sheet 76,677, Utah); and *Hierochloë odorata* (Forest Service sheet 18,942, Utah).

lands. Farming decreased, and the fields gradually reverted to brush and forest. In turn, the marshes were probably subjected to less frequent mowing. Fires again may have occurred, but probably not with the frequency of Indian times.

5. The Ditching Period. The addition of ditching created still a further complicating factor. In the Barn Island Area, ditching was begun in 1931 and completed the following year. Since then, the ditch system has been maintained, although various irregularities due to temporary blockage have occurred. In general, the ditches appear to change soil and water levels, to alter the local pattern of drainage, and to offer a new avenue of invasion for Iva. In this present period, fire does not seem to be a significant factor, but mowing still occurs on several of the valley-marshes.

Upland Vegetation of the Vicinity

The upland forest of the vicinity is primarily an oak-sprout forest, with a heavy admixture of hickory. Black oak, white oak, shagbark hickory and bitternut are common. Pitch pine is rare. Beech is rare, found only on favorable sites. Black gum (Nyssa) is common along the edges facing the ocean. Thickets are typical on abandoned agricultural lands and are frequently well consolidated by catbrier (Smilax). In such thickets, dwarf sumach, sassafras, high blueberry (*Vaccinium corymbosum*), roses and many other shrubs are common. Grasslands around abandoned farms are often dominated by *Agrostis alba* or by *Andropogon scoparius*. Occasionally, when the grasslands face the ocean, *Andropogon furcatus* and *Sorghastrum nutans* will be frequent. *Andropogon scoparius, A. furcatus* and *Sorghastrum nutans* are three of the most important dominants of the prairies of the Middle West, and here emerge into dominance in the absence of woody species. Such a condition implies some interesting relationships between the vegetation of these two otherwise contrasting areas.

Between the tidal-marsh and the upland forest is frequently a narrow shrub border composed of various upland species which predominate as a community in this exposed storm-swept band. They are frequently killed back by exceptional saline conditions. At one locality near the Brucker Marsh, this shrub border is mowed and as a result has been replaced by grassland of *Panicum virgatum*.

Freshwater swamp often bears a red maple forest. Such forests were strongly affected by the 1938 hurricane, which not only broke many of the trees, but presumably caused varying amounts of kill by excessive salinity. Open swamps are covered with cattail.

Vegetative Identification of Some Grasses

One of the chief problems in the vegetational study of the tidal-marshes is recognition of the grasses when not in flower and fruit. This situation is true for all grasses in spring and early summer, and for certain species on certain sites throughout the growing season. To facilitate such identification, drawings of significant features have been prepared by L. Hughey, U. S. Forest Service (Fig. 5). *Juncus gerardi* is included because of its similarity to grasses at early stages of growth.

VEGETATION: COMPOSITION AND STRUCTURE

General Aspects

At first glance, the tidal-marshes are a vast flat monotonous expanse of somber grassland, cut by deep meandering estuaries, and shallow man-made ditches.

After that first glance, however, the marshes become an interesting complicated bewildering mosaic of various distinctive and clearly demarcated plant communities. Tall *Spartina alterniflora* borders the bay, the ditches, and the estuaries. *Panicum virgatum* and its associates border the uplands and appear around "islands" and emerging rocks. Masses of Juncus alternate with stretches of *Spartina patens*. Beds of Distichlis appear almost anywhere. Stretches of forbs, often Plantago, Limonium or Triglochin, appear here and there. Relatively circular areas of dwarf *Spartina alterniflora*, shallow pools, or even bare spots are common. Large glacial boulders are scattered about. Tidal trash, potholes, and cowlicks are encountered where least expected. It is amazing that almost all these various communities remain very clearly segregated from each other: the amount of area occupied by ecotones is relatively small. In this respect, the authors know of no other area in North America or elsewhere, where distinct communities occur in such a complicated mosaic on such a small scale.

One is tempted to feel that this remarkable mosaic should be interpretable in terms of ecologic factors. If so, our present knowledge is as yet far from sufficient. It is very likely that contemporary concurrently acting factors are only partially responsible for present distributions. In other words, single abnormal catastrophic factors may have produced effects lasting into the present; and general past conditions may have been such that the vegetation still reflects them. In these respects, the present mosaic may be thought of as a momentary expression, different in the past, destined to be different in the future, and yet as typical as would be a photograph of moving clouds.

For purposes of description, the tidal-marshes will be considered first as a simplified theoretical landform extending from the upland to the sea, possessing surface drainage, without benefit of estuaries, ditches, rocks, islands, undrained pannes, pools, erosion spots, levees, and other such phenomena. These other phenomena will then be discussed separately. The reader may then combine these details to reconstruct the varied mosaic that is the tidal-marsh.

The Upland-to-Bay Sequence

In a theoretical upland-to-bay sequence, unmodified by all the complications which invariably do occur,

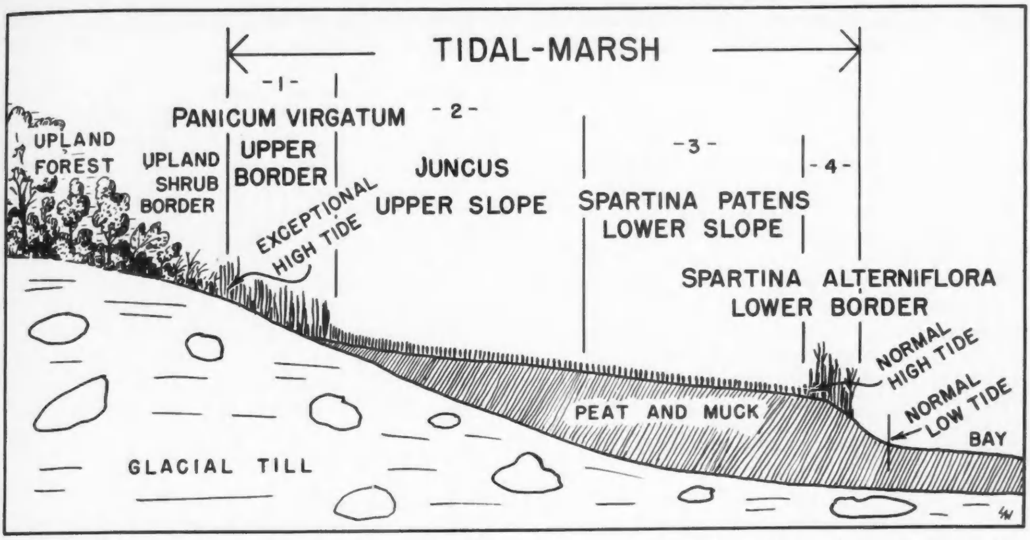


FIG. 6. Diagrammatic cross-section of the upland-to-bay sequence, showing the characteristics of the major vegetational units. Vertical scale much exaggerated.

the following communities[6] will be found (Fig. 6):

Upland Forest. The forest is described briefly in the introduction to this paper.

Upland Shrub Border. The shrub border may be absent on steep slopes where the trees overhang the marsh.

1. The Panicum virgatum Upper Border. A narrow belt of tall grasses on peat. Soil level is considerably higher than that of the general marsh.

2. Juncus Upper Slope. A relatively pure stand at the higher marsh levels, possessing surface drainage after each tide that covers it.

3. Spartina patens Lower Slope. A relatively pure stand at the lower marsh levels, possessing surface drainage after each tide that covers it.

4. Spartina alterniflora Lower Border. A fringing belt occupying the wave-cut bluff, transitional to the mudflats of the bay.

Past botanical literature has frequently recognized *Distichlis spicata* as forming a distinctive plant community. In the area studied, Distichlis has a very wide ecologic tolerance. It is found in practically all the communities, seldom pure except on sites which it has recently invaded. It appears to enter the Juncus, and especially the *Spartina patens* types as ecologic equivalents of those dominants, but rarely does it approach them in their high degree of coverage. For present writing, it does not seem reasonable to accord it a special zonal status.

This basic sequence of vegetation belts has been partially implied or stated by past researchers. No researcher has reversed any part of the sequence as given above. The basic features of the sequence were recognized by Chapman (1938), Harshberger (1916), Johnson (1925), Nichols (1920), Townsend (1925), and Transeau (1913).

[6] *Community* is any group of plants living together, exhibiting some degree of integration as an organized whole or "organism." The term "association" is linked with several rigid definitions, giving it a hierarchic rank in as many iron-clad philosophic systems of vegetation science. To avoid confusion, the term is not employed as a vegetational concept in this paper.

PANICUM VIRGATUM UPPER BORDERS

In general appearance, the Upper Border community forms a distinct narrow belt between the tidal-marsh proper and the uplands. It varies from 0-20 or more meters in width, although most frequently it is 7-10 m. wide. The vegetation is a tall dense grassland 1-2.5 m. high, most often of Panicum virgatum. Locally the Panicum is scarce or absent, and in such cases *Spartina pectinata* is usually predominant. On Barn Island itself, *Tripsacum dactyloides* holds the same dominance as does Panicum elsewhere. The Panicum community is a tussock grassland, with the spaces between the tussocks filled with various other small plants, or completely covered by dead grass which thus forms a natural mulch.

Panicum virgatum and *Spartina pectinata* are two of the most distinctive dominants of the slough-grass type of the typical prairies of the Middle West. In this respect, the Upper Border community holds an interesting relationship to these so-called "climatic" grasslands that is beyond the scope of this study. The relationship is perhaps of the same category as that between the local upland grassland of *Andropogon furcatus, A. scoparius,* and Sorghastrum, and the mid-west prairies dominated by the same species.

The substratum of the Panicum Border is usually an organic peaty material 10-50 cm. in depth, overlying the glacial till. This statement is based on repeated surface observations and on some half dozen scattered excavations. The soil surface is approximately 0.5 m. above that of the general tidal-

marsh, and thus this Border is evidence of the building of an organic substratum above the "normal" marsh level. Wherry (1920) found that this belt, near Revere, Mass., was highly acid in reaction, in contrast to the moderate alkalinity of the general marsh.

It is inferred that the Panicum Border is subjected to rare and catastrophic tidal effects. For example, the presence of flotsam trash, the frequent occurrence of young shrubs, the occurrence of old large dead shrubs, all imply repeated setbacks and active developmental trends. Finally, accepting the theory of post-glacial submergence of the coast-line, we must also accept the theory that the Panicum Border has gradually shifted landward, invading the upland on the upper landward side, and being invaded by Juncus marsh on the lower seaward side.

Mowing is apparently of great importance in this community, and the effects are discussed in a later section.

It is purely a matter of arbitrary decision as to whether the Panicum Border is considered a part of the tidal-marsh or a part of the upland. It belongs to the marsh on the basis of its substratum, the life-form of its dominants, and its tidal controls. It belongs to the uplands on the basis of its complex flora, and the life-form of its shrubby species that tend to become dominant.

A certain segregation is sometimes evident within the Border, especially where *Cladium mariscoides, Eleocharis rostellata,* and *Scirpus americana* are common. At such times, the floristically complex Panicum section is uppermost on the land side; Cladium is predominant in a more open and lower middle section (and may be absent from the adjacent upper side). Eleocharis and Scirpus are predominant in the lowermost seaward side which, except for these two species, is otherwise typical lower marsh.

The composition and structure of the Panicum Border were studied in a series of 26 10-sq.-m. plots, scattered around the entire margin of the Brucker Marsh. The twenty-six plots, making a complete circuit around the marsh, were taken on July 15, 28, and 29, 1947. Each plot was located at random, and was circular in outline. Approximately equivalent elliptic plots were used when the Border was exceptionally narrow. For each plot, a floristic list was made, and relative abundance designated by three categories:

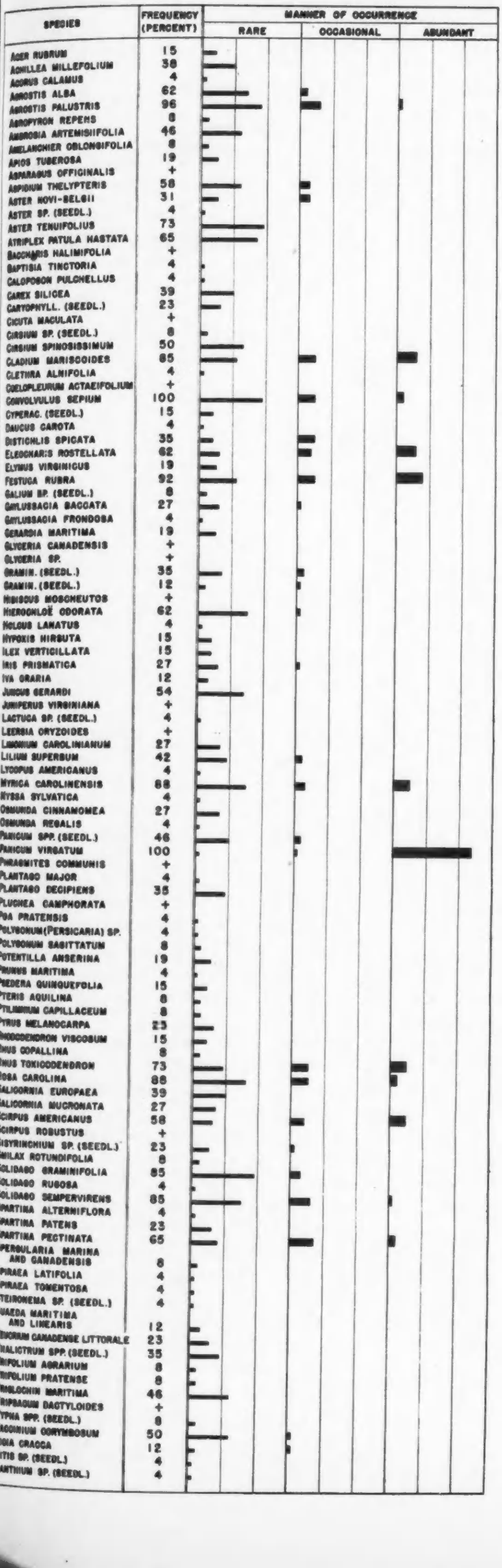
R rare
O occasional
A abundant

Such a 3-fold system has certain disadvantages, for it seeks to combine Density (number of stems per unit area) with Coverage (actual area covered by a plant), leading to a large subjective error in those cases where a plot may contain one or two plants of great Coverage, or a great number of minute plants of almost no total Coverage. Nevertheless, the system has many advantages for simple rapid survey.

These plot data are summarized in Figure 7. The 26 plots are considered as samples of a single Stand. This Stand is considered to have been chosen at random from those of the general area. In the figure, the number in the first column represents the percentage Frequency (the relative number of times a species occurs in the quadrats of a single Stand). A "+" indicates the species occurred in the community outside of the quadrats. The solid bars, representing the "manner-of-occurrence," are proportional in length in the number of plots in which that species occurred at that particular degree of abundance.

This analysis of the Panicum Border reveals both its individuality and its relationship to other communities. The distinctiveness of the Border is related to the abundance of *Panicum virgatum,* and the lesser abundance of *Spartina pectinata.* The local abundance of Tripsacum outside the plots is equally distinctive. All three grass species show a high Fidelity to this community, being found rarely if at all in the uplands or in the tidal-marsh proper. Other species of high Fidelity—as based on occurrence here and elsewhere in southern Connecticut—include: *Agrostis palustris,* Baccharis, Cicuta, *Cirsium spinossimum,* Cladium, Elymus, Hierochloë, *Iris prismatica,* Iva, *Lilium superbum,* Ptilimnium, *Solidago sempervirens,* and Teucrium. Practically all the tidal-marsh species are present: *Atriplex patula hastata, Distichlis spicata, Gerardia maritima, Juncus gerardi,* Limonium, *Plantago decipiens, Salicornia* spp., *Spergularia* spp., *Spartina alterniflora, Spartina patens, Suaeda* spp., Triglochin. Of these species, *Spartina patens* grows 2-3 times as tall here as in the lower tidal-marshes, in an environment less saline than in those lower marshes. The annual *Aster subulatus* was not found here or elsewhere in the area. Freshwater swamp species enter: *Acer rubrum,* Acorus, *Aspidium thelypteris,* Clethra, Eleocharis, Ilex, Lycopus, *Osmunda* spp., Rhododendron, Scirpus, and Typha. Upland field and weed species come in: Achillea, *Agrostis alba, Agropyron repens,* Ambrosia, *Aster* spp., Cirsium, Convolvulus, Daucus, Festuca, Lactuca, *Panicum* spp., *Plantago major, Polygonum* spp., Pteris, Sisyrinchium, *Solidago* spp., *Spiraea* spp., Vicia. Finally, upland scrub and forest species tend to enter, or to be vestigial: Acer, Amelanchier, *Gaylussacia* spp., Juniperus, Myrica, Nyssa, Prunus, Psedera, Pyrus, *Rhus* spp., Rosa, Vaccinium, and Vitis.

Scirpus-Typha Brackish Spots. Freshwater springs are found occasionally along the shores, some of which have been excavated and developed in the past as wells and water-holes. The vegetation is markedly different in the immediate vicinity of these water-holes, even though there is no apparent overflow of fresh water. For distances up to 15 meters from the site may be found a dense band of Typha. Seaward occurs a second band, of Scirpus (probably *S. robustus*), lower in height and more open in cover. The density of each of these species appears to pre-



clude the development of the other species of the Panicum Border. Salinity of the soil solution is worthy of investigation at these sites.

Flotsam Spots. Accumulations of tidal trash are apt to be deposited anywhere within the Border by storm tides. These spots are up to 5 m. in length, and are frequently thick enough to kill the buried plants. On the surface are apt to be found various species having wave-borne propagules, including Xanthium, Suaeda, Atriplex, Cakile, and Salsola. No evidence was observed to indicate that these spots lead to subsequent disintegration of the underlying organic substratum. It would appear that as the flotsam disintegrates, the space is reinvaded by species of the Border.

JUNCUS UPPER SLOPES

The Juncus community occurs typically as a marginal band 7-10 meters wide, just below the Panicum Border, following the curvatures of the coast-line. In this position, it is distinctly an "upper slope" type. It is also found in areas of all shapes and sizes scattered through the marsh, wherever the local conditions are presumably the equivalent of those of the Upper Slope.

The community is readily separable on the landward side from the much taller and floristically complex Virgatum Border. On the seaward side, the dense sward gives way to several other types, usually with knife-edge abruptness.

The general appearance of the Juncus community is that of a dense practically pure "grassland." At first glance, it appears to have no accessory species whatever. Those which do occur, occur so sparsely that their Coverage is insignificant. Distichlis occasionally becomes common, but when so, Juncus is still predominant. The color differs at different seasons, but whether it is greenish, blackish, or brownish, it is always distinctive from adjacent types.

The structure and composition of the Juncus community were studied in a series of 50, randomly chosen, 10-sq.-m. plots scattered in the marsh in front of headquarters. Plots were taken on August 26 and September 13, 1947. Data are shown in Figure 8. Many of the secondary species are only to be found by diligent searching. The abundance of Iva is to be noted. Iva seedlings are frequent, but usually they are small and rarely do they give evidence of continuing to grow into large shrubs, except in the vicinity of other large Ivas where the Juncus is thin. The various other herbs which are found within the Juncus community are generally slender individuals, appearing as if growing under strong competition. *Spartina patens* occurs within the community, but only with an insignificant Coverage. There is no

FIG. 7. Frequency and manner-of-occurrence of the species of the Panicum virgatum Upper Border. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence. A + indicates the species occurred in the community outside of the quadrats.

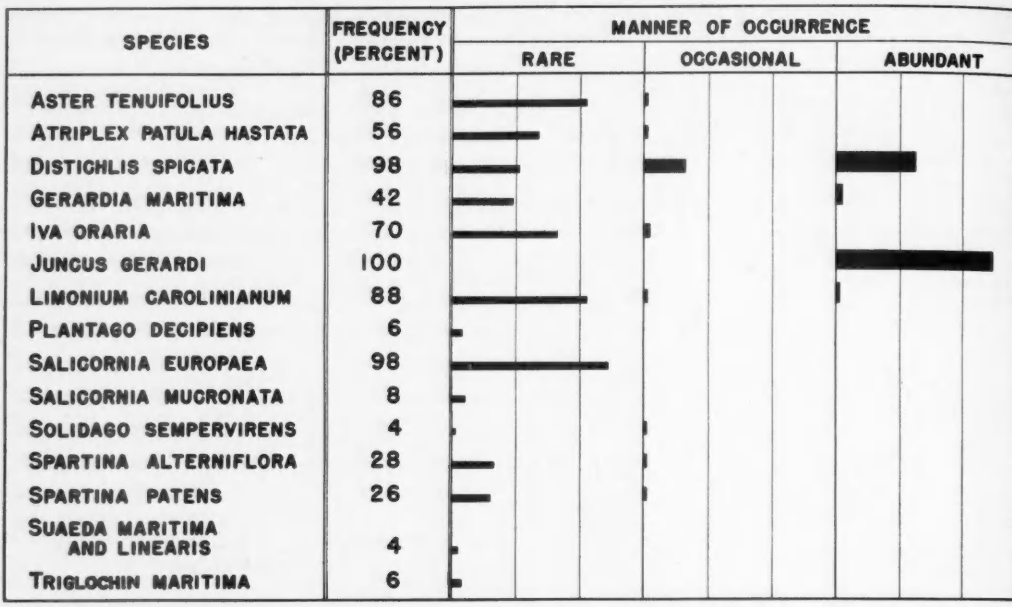


FIG. 8. Frequency and manner-of-occurrence of the species of the Juncus Upper Slope. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence.

gradual transition between the distinctive Juncus and patens communities.

The Juncus appears to create a closed, saturated, stable community, producing such a dense cover that few other plants can gain entrance or persist within it. Although Juncus terminates abruptly when it borders such open types as the Forb Panne, there is no obvious evidence that the Juncus is extending its range.

On a time-scale to be correlated with physiographic change, one must assume that the Juncus belt has gradually moved landward. In this respect, it has slowly invaded the Panicum Border on the upper side, and has been invaded by the *Spartina patens* community on the lower side. Whether such invasion occurs uniformly or irregularly is not known.

Flotsam Spots. Masses of tidal trash are found repeatedly in the Juncus community, often thick enough to kill the Juncus below them. The future development of such spots is not known. There is no evidence on the area however that they develop into potholes, decay areas, or other types of edaphic disintegration.

Cowlicks. The dense masses of Juncus are apt to become matted and flattened at the end of the season, through winds and tides. These very distinctive spots have been called "cowlicks," from their fancied resemblance to a cowlick on one's head, that is, "a tuft of hair turned up or awry (usually over the forehead), as if licked by a cow" (Webster's Dictionary, 1948). There is no obvious evidence on the area that the vegetation of the succeeding season is in any way affected, and that the cowlick is genetically related to potholes, pannes, or other local phenomena. Cowlicks occur more commonly in the Patens Border.

SPARTINA PATENS LOWER SLOPES

The Spartina patens Lower Slope occurs very typically inland from the Spartina alterniflora Lower Border. It also occurs in areas of all shapes and sizes scattered over the marsh, wherever the local conditions are reasonably equivalent to those just inland from the Lower Border.

The community is readily separable on the seaward side from the *Spartina alterniflora* type, which grows taller and has much coarser and ranker foliage. Elsewhere, the dense mat of patens ends abruptly, giving way in a matter of a few inches to the Juncus community, the Forb Panne, or stunted *Spartina alterniflora* of the pannes.

In general appearance, the Patens Slope is that of a dense essentially pure grassland. Like the Juncus type, it appears at first to have no accessory species whatever (except for the irregular occurrence of Distichlis). Those species which do occur, are thinly interspersed and have a very low Coverage. The green shade of the grassland varies during the season, but is distinctive at all times, and emphasizes the mosaic nature of the tidal-marsh.

The structure and composition of the Patens Slope were studied in a series of 50, randomly chosen, 10-sq.-m. plots scattered in the marsh in front of headquarters. Plots were taken on September 13 and 27, 1947. Data are presented graphically in Figure 9. The floristic similarity of this community with that of Juncus is to be noted. The major difference is in the respective dominance of their "name" spe-

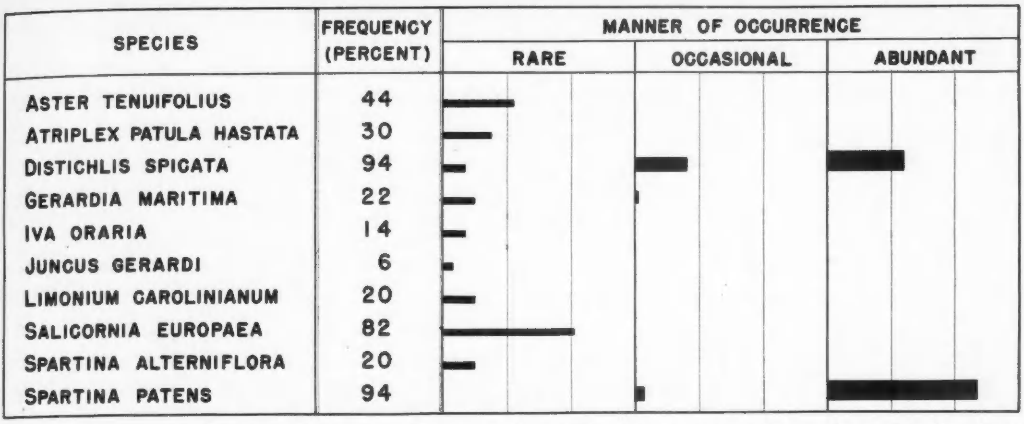


FIG. 9. Frequency and manner-of-occurrence of the species of the Spartina patens Lower Slope. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence.

cies, that is, Juncus and *S. patens*. Only patens and Distichlis ever become abundant in the Lower Slope. The Coverage of Distichlis however is rarely high, and rarely more than 50 percent. With few exceptions, all other species are "rare." Juncus does occur, but only sporadically: its relative absence is a striking phenomenon, considering its pure dominance so nearby. Iva is found repeatedly, not as often as in the Juncus slope, but here also it occurs only as seedlings, and does not appear to develop into taller plants except where the Spartina is thinned out by shading. The absence of *Salicornia mucronata* may or may not be a local coincidence.

The Spartina appears to create a closed saturated stable community, producing such a dense cover, which mats down so heavily—even more so than Juncus—that few other plants can gain entrance or persist within it. Although it terminates abruptly where it borders such open types as the Forb Panne, there is no obvious evidence that the Spartina is extending its range into those forbs.

Flotsam Spots. Masses of tidal trash are found occasionally, though less often than in the Juncus Slope. It appears that as soon as the material disintegrates to a certain extent, subsequent tides wash it away. There was no evidence on the area that these spots remain bare or develop into other phenomena.

Cowlicks. Wind-blown and tide-flattened areas commonly occur toward the end of the season. No evidence was observed that such cowlicks permanently affect the vegetation, despite the temporary density of the matted grass.

Peat-hummock Type. A most unusual and interesting phenomenon occurs at the heads of the "valley-marshes," in a position just seaward of where the tidal-marsh changes to freshwater cattail swamp. For example, as one walks upstream, the extraordinary flatness of the tidal-marsh peat abruptly gives way to an extremely hummocky surface. No longer can one find flat footing: each step is at some angle on the sides of a small hummock. The actual relief is probably 20-40 cm. In about half the stations, the change from flat to hummocky surface occurs at an old stone wall, which there crosses the marsh. Strangely, the plant community itself does not change as one enters this hummocky surface. Both hummock tops and depressions are uniformly covered with *Spartina patens* andor Distichlis. The Distichlis is often pure. (Distichlis is known to survive over patens, when the two in mixture are subjected to freshwater influences.) Farther upstream, both hummocks and tidal-marsh plants give way to flat freshwater cattail swamps.

Any valid interpretation of this phenomenon must rest on future studies of the nature of the peat in the hummocks. As a working hypothesis in the meantime, and on the assumption of recent increase of effective high-tide levels, one must assume that the hummocky area was a freshwater swamp at a relatively recent period, possibly in colonial days. That it was hummocky as well demands the existence of some hummock-producing community, something not now existing in the flat cattail swamps adjacently upstream. Conditions would be fulfilled by hypothesizing the existence of a freshwater tussock swamp of sedges and rushes, such as may come into existence under conditions of grazing. It is suggested, therefore, that the peat hummocks of this type of tidal-marsh may be the "fossils" of a previous vegetation, a freshwater community that existed at a lower level of effective tides, and possibly under the influence of colonial grazing. Since those times, the grazing has ceased, even in adjacent upstream freshwater marsh, and the tides have flooded the area and fostered the tidal-marsh community.

SPARTINA ALTERNIFLORA LOWER BORDERS

The Spartina alterniflora community occurs very typically as a thin fringing line along the bluff-like bay front of the tidal-marsh, usually about 2 meters wide, wider only in cases of shallow aggrading areas.

It is also found along almost all estuaries and many mosquito-ditches.

The land surface of the community is obviously at a lower level than the remainder of the tidal-marsh, evident from the fact that it is flooded at every high tide. The community is on a sloping drained surface, and occupies the upper half of that bluff-like drop from the tidal-marshes down to the muddy tidal flats of the bay (Fig. 6).

This tall community is readily separable vegetationally from the relatively bare mud flats on the one side, and from the fine grassy vegetation of lower stature, at a higher soil level, on the other side.

In general appearance, the Alterniflora Lower Border is a rank coarse pure grassland. Even more so than in the other tidal-marsh communities so far described, the accessory species are very few; they appear to be "accidentally" present, and their Coverage is practically negligible.

The structure and composition of the Lower Border were studied in a series of 50, randomly chosen, 10-sq.-m. plots in the marsh in front of headquarters. Sampling was from estuary-borders and ditch-borders in the absence of sufficient bay-front sites at this place. Plots were taken on September 13, 1947. Data are presented graphically in Figure 10. Seldom is a community as mono-specific as this.

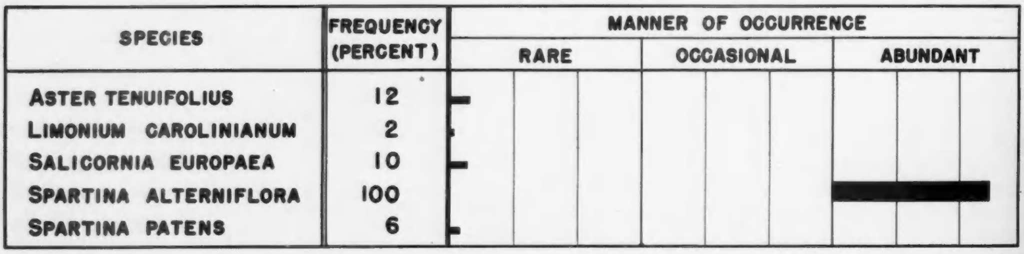


FIG. 10. Frequency and manner-of-occurrence of the species of the Spartina alterniflora Lower Border. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence.

Spartina alterniflora is continuously abundant; only four other species were found in the quadrats, all appearing as temporary and accidental from other communities a few meters away.

From a chronologic point of view, the Lower Border is a temporary vegetational phenomenon. On a stable substratum, the community quickly builds up a dense peaty mat of coarse roots that soon reaches a surface level which will allow the *Spartina patens* community to take over. On the other hand, wave erosion on the bay front may remove the community, or prevent its development. For these reasons, all degrees and combinations of erosion and aggradation are observable. The width of the border, the slope of the substratum, and the occurrence of other species as pioneers or relicts reflect such complex histories.

DEPRESSIONS: PANNES AND POTHOLES

THE PANNE[7] SEQUENCE

A noticeable characteristic of the tidal-marsh mosaic is the occurrence of numerous patches of vegetation, circular, near-circular, or elliptic, or of various combinations of circles within circles, or of interlocking circles. In pre-ditching days, these may have occupied up to 20 percent of the total marsh area, occurring as broad swales lying between the upland on one hand, and the natural levees of bay front or estuary on the other hand. The vegetation of such circles is concentrically arranged in a very obvious fashion. The center of the circle is frequently open water, or mud with or without crystallized salts at the very center. Vegetational belts appear more and more favorable in growth the farther they are from the geometric center.

From the observations of the above paragraph one may infer that surface-water levels are correlated with these vegetational phenomena. Further observations establish the inference almost indubitably. The margins of existing pools are more or less equidistant from the borders of the concentrically arranged communities. When high tides flood some of these areas, the water levels of these temporary pools are in accord with lines demarcating the communities. Even the highest of the panne communities, the Forb Panne is usually flooded at high tides when adjacent normal marsh is dry. Where tidal encroachment covers both Forb Panne and normal marsh to apparently equal depths, the condition seems to be due to recently altered levels. Such minor changes in level are known to be in actual progress over much of the marsh.

The effect of these surface-water levels on plants is considered to be mainly a matter of the sporadically occurring lethal concentrations of salts, accumulated by progressive evaporation. In this respect, the distribution is not in accord with contemporary ecologic factors, but shows a degree of development

[7] *Panne*, any small shallow depression in the earth and its distinctive vegetation. Tidal-marsh panne, a shallow undrained depression in the marsh, bearing distinctive vegetation. The French spelling is preferred, on the basis of priority, and to distinguish it from many other English pans.

subsequent to isolated historic events. Good supporting evidence for this theory was offered by an "experiment" unwittingly carried out in the marshes seaward of Dike 3. In this area, a mosquito-ditch was accidentally plugged in the spring of 1947. Following one or several high tides which overrode the plug, an irregular area of approximately one acre was flooded. This area had been covered with dense *Spartina patens, S. alterniflora,* and forb communities. Apparently the water remained trapped, and gradually evaporated, reaching lethal concentrations. Observations in midsummer 1947 showed a complex series of killed areas and variously decomposed plant communities, all in concentric belts, with curving arc-like borders implying particular water levels (Fig. 11). The upper limit of kill was a knife-edge border: totally killed and totally unaffected masses of plants appearing within radial distances of a few centimeters. Highest zone of kill was dead *Spartina patens,* with the foliage matted and flattened by dried algal scums. At lower levels both Spartinas appeared browner and more decomposed, as if they had been under water for a longer time. At still lower levels, decomposition had progressed further, and white incrustations of salt appeared at the circular center of the depression. Nearby, a quadrat (fortunately though coincidentally placed here the previous season) showed a complete transformation from a typical Forb Panne to the next lowest in the sequence, the Stunted Spartina alterniflora Community.

FIG. 11. Killed areas of *Spartina patens* (appearing smooth) and stunted *S. alterniflora* (appearing rough) in new pannes, created by the blocking of a mosquito ditch. At Dike 3, looking southeast from Photo-station 23.

On this quadrat, every species except *S. alterniflora* had died, and their remains were found only with difficulty.

During the spring of 1948, this area filled with water, which evaporated to dryness by midsummer. In early autumn, it was again filled with tidal waters. Much of what had been stunted alterniflora is now a Salt Panne, with scattered Salicornia. Areas of Forb Panne are now bearing stunted alterniflora. Some of the patens belt is entirely destroyed. A new line of alterniflora is appearing locally at the edge of the killed patens belt. In summation, the recent changes may be considered as a destruction of the belts, with reformation under conditions of higher salinity extremes, that is, a centrifugal shift of the belts. If these extremes vary from year to year, it is to be expected that the belts would tend to oscillate accordingly.

Even further inferences may be drawn concerning the antecedent history of this interesting area. Without evidence to the contrary, it may be assumed that most of this newly killed area had been, in pre-ditching days, a relatively bare undrained depression, with or without a permanent Ruppia pool. Ditching had converted the site into a drained surface, which then was gradually invaded by the communities of the normal slope. Plugging of the ditch caused the reversion just described.

The origin of these undrained depressions may be attributed to one or more of several factors. *1,* levee-like deposition around the borders of an area, such as deposition at the margins of estuaries and of ditches, by the waters of those channels. *2,* compaction and settling of the marsh peat at the center of the area. Although no indisputable evidence was obtained to show that such compaction occurs, the hypothesis is useful, has been proposed by others, and is not unreasonable in interpreting the distribution of many of the pannes. *3,* coalescing tussock-forming plants, enclosing a panne with a high rim. Arneria has this role in England, but no such plant is known in New England. Although certain pannes are now rimmed with *S. patens,* it does not appear that this species develop its own high rim about the panne. To some extent, however, the adjacent peat-building Juncus and *Spartina patens* may have an analogous role in that the entire marsh level is raised while the panne remains at the same level. *4,* American literature repeatedly emphasizes the role of cowlicks and flotsam spots in initiating pannes. Although the present authors do not deny such a genesis, there was no evidence for it on the area studied. *5,* decay of underlying peat, giving rise to potholes (described later). In view of the fact however, that the substratum of pannes is typically hard and firm, the authors are not yet ready to hypothesize a successional relationship between potholes and pannes on the area. *6,* the closing of meanders to form oxbows, and dammed ditches, and vestigial pools left by *S. alterniflora* when rapidly colonizing a mudflat. All these processes could reasonably give rise to pannes.

Communities of the pannes are well segregated and easily differentiated in the field. Four units are here described (Fig. 12): *a,* Ruppia Pools, *b,* the Salt Pannes, *c,* the Stunted Spartina Alterniflora Community, *d,* Forb Pannes.

Ruppia Pools

Shallow pools still occur, though rarely, in the marshes near the bay front, despite the thoroughness

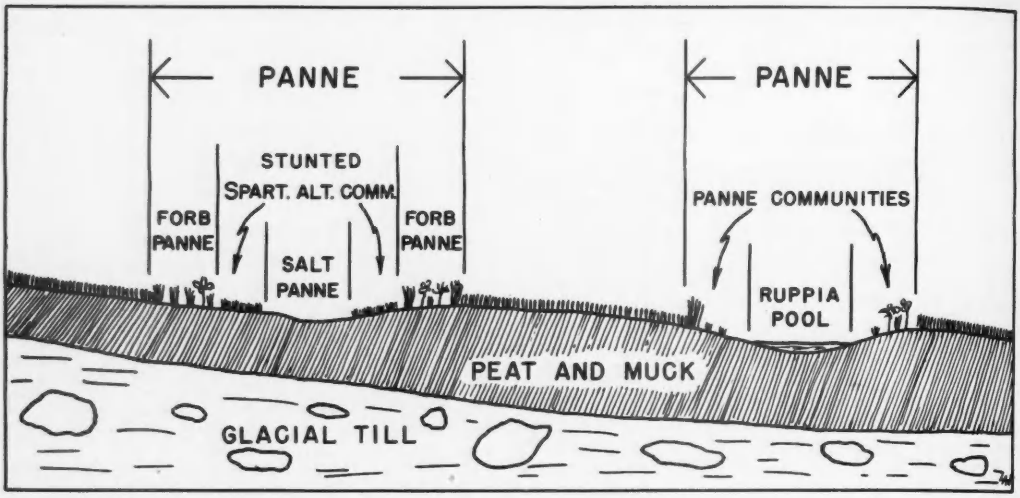


FIG. 12. Diagrammatic cross-section of the panne sequence, showing the characteristics of the major vegetational units. Vertical scale much exaggerated.

of the mosquito-ditchers. The water in these pools is seldom more than 30 cm. deep; and the bottoms are relatively hard and firm. *Ruppia maritima* typically occurs in dense masses, occupying from 1-30 percent of the area. At certain seasons of the year, thick algal scums cover much of the surface. These were not studied, but are believed to be composed of numerous species, complexly organized as a community of their own.

Salt Pannes

Salt Pannes are those essentially devoid of all higher seed plants. They occur as small roundish spots 1-10 meters in diameter, sometimes much larger, with remains of heavy algal scums encrusted on the surface, often themselves covered with crystallized salts.

Within several miles of the area are similar sites bearing colonies of annual *Salicornia europaea* andor *S. mucronata*. These halophytic annuals are able to invade such bare sites in favorable seasons and form temporary communities that may not reappear the following year.

Stunted Spartina alterniflora Community

The Stunted Spartina alterniflora Community occurs very typically as an intermediate zone in the pannes, with the Forb Panne centrifugally and the Salt Panne centripetally from it. Where the Salt Panne is absent, this community occupies the center of the depression.

The inward edge of the Alterniflora Community is easily delimited in terms of the last occurrence of the name-species itself. The outward edge is clearly observable on the land, and is identifiable not so much in terms of a change in alterniflora as in the regular presence of a good growth of various forbs.

In general appearance, this Alterniflora Community appears to be a pure stand of stunted sparsely distributed individuals. Height varies from 10-25 cm.; color is yellowish and suggests unfavorable growth conditions. Associated species are few and far between, and of no significant Coverage. Although this community is very similar to the Alterniflora Lower Border in the predominance of the Spartina, the resemblance ceases there. In the one community, the grass is tall, dense, and luxuriantly growing; in the other community, it is short, sparse, and depauperate. The two sites are completely different, and are almost never contiguous.

The structure and composition of the Stunted Spartina alterniflora Community were studied in a series of 50, randomly chosen, 10-sq.-m. quadrats in the marshes seaward of headquarters. Plots were taken on August 10, 1947. Figure 13 shows the complete preponderance of the name-species. Nine other species occur so sporadically and so rarely as to be of little importance. It may be of significance that *Spartina patens* did reach an occurrence noted as "occasional." This condition may imply a genetic relationship to the Patens Lower Slope, either as vestiges of a past condition or as potentialities for a future condition. That Juncus did not occur is in line with the role of this species as an upper-slope plant.

In accord with the evaporation hypothesis of panne vegetation, this community would tend to be invaded by the Forb community in intervals between salt-killings. Such periodic killings would set back the vegetation to the Stunted Alterniflora phase, or even to a Salt Panne. In accord with the theory of a rising sea-level, the entire marsh surface has been rising by peat accumulation, while parts of it periodically settle due to consolidation and compaction of the peat. For these reasons, the life of any one panne is probably temporary, although the average number of pannes on a marsh remains the same.

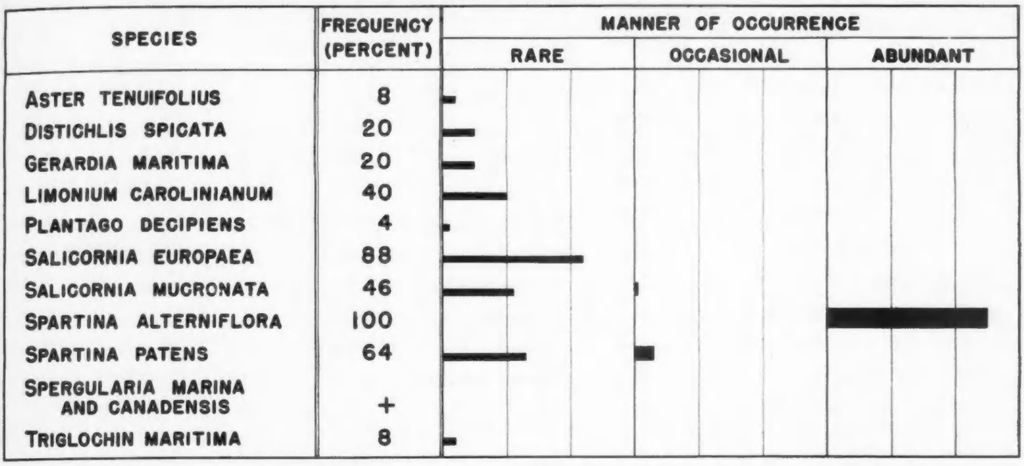


FIG. 13. Frequency and manner-of-occurrence of the species of the Stunted Spartina alterniflora Community. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence.

Forb Pannes

The Forb Panne occurs very typically in the panne sequence centrifugally from the Stunted Spartina community. It also occurs in highly irregular areas over the tidal-marsh, areas which are often oriented with reference to ditches and estuaries and are clearly referable to the panne sequence in the light of the deposition that occurs along the banks of these modern water channels.

The Forb community may be bounded in one direction by the dense sward of the Patens Slope with its few and slender competition-affected forbs. In another direction, it may be bounded by the open Stunted Alterniflora community, also characterized by very few and poorly developed forbs.

In general appearance, the Forb community is the most variable and most colorful of the tidal-marsh associations. It is here that the famous herbs flower and fruit to best advantage. In one area, Limonium may be predominant, in another Triglochin, somewhere else Plantago, and in still another site Gerardia or Aster. Despite these variations, there seems to be no valid basis for recognizing more than one community. The differences are intergrading and appear to be due to differences in priority of invasion, or to chance and coincidence rather than to major ecologic controls.

The structure and composition of the Forb Panne were studied in a series of 50, randomly chosen, 10-sq.-m. circular plots, in the marshes seaward of headquarters. Plots were taken on August 10 and 26, 1947. Figure 14 well illustrates the variability of this association. Eight species attain the condition of being "abundant," implying their pure or mixed dominance locally. With one exception (Juncus, of the Upper Slope) all the species have a high Frequency, indicating a certain stability and equilibrium of the stand. The presence of a small amount of alterniflora indicates the facility with which this type can be converted into a Stunted Spartina phase, a conversion already described.

A comparison of Fig. 14 (Forb Panne) and Fig. 13 (Stunted Alterniflora Community) is of considerable interest. If Juncus is eliminated from the former (a rare element, in only 5 plots) two communities of identical floristic composition are found, but of vastly different structure, appearance, and ecologic conditions. In the Forb community, all 10 species have Frequencies of 64 percent or more, with half of them at 100 percent. Eight of the species can become "abundant" and can predominate locally. In the Stunted Community, eight species have Frequencies of 64 percent or *less* (the 88 percent Frequency of the annual Salicornia may have been purely local), and five of the eight have Frequencies of 20 percent and less. Only the name-species has a Frequency of 100 percent, and becomes "abundant," thus predominating at all times.

POTHOLES

"Potholes" as here used are deep vertical-sided pits varying from 1-30 meters across, usually filled with standing water, with bottoms at or below low-tide levels, composed of slimy, oozy, decomposing malodorous muck. They have also been called "rotten spots" in the botanical literature.

No theory is put forth as to the genesis of these potholes. Previous investigators have linked them with flotsam spots, cowlicks, and Salt Pannes. No intermediate stages have been found by the authors, however, connecting such phenomena to potholes. Basically, potholes should be either "primary" (dating back to days of open lagoon water) or "secondary" (arising by decomposition of the marsh peat). A primary origin is not impossible, though improbable, as present evidence of tidal-marsh history calls for a freshwater marsh in the areas where

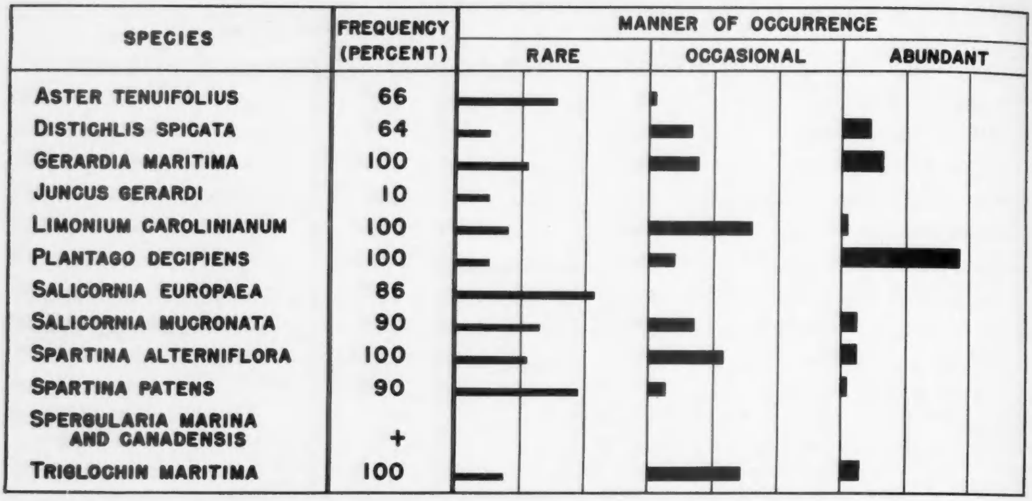


FIG. 14. Frequency and manner-of-occurrence of the species of the Forb Panne. The length of the bar is proportional to the number of quadrats showing the respective degree of occurrence.

potholes exist, rather than a salt-water lagoon. Fresh-water pools admittedly may have existed, and been perpetuated. The fact that some potholes appear to be enlarging at one side would imply a very long development. In view however of the general over-all abundance of peat-forming alterniflora, it is difficult to believe that any one pothole could survive more than a few hundred years without significant secondary effects. As to a secondary origin, this would imply disintegration of the peat from the surface down, or from below up, causing eventual collapse of the surface. No evidence of surface disintegration has yet been found. Evidence of subsurface disintegration is inconclusive. Areas of marsh do occur in the region which are distinctly quaking, as a northern bog, especially at high tide. In a marsh some ten miles to the west, a surface mat of alterniflora occurs, fringing open water. Whether this mat is encroaching over the open water, or whether it is vestigial and remaining from subsurface decomposition, is uncertain without further investigation.

In the potholes on the area—of which some six have been noted—both contraction and enlargement appear to be taking place, in some cases in the same pothole. For example, one side appears to be being invaded by *S. alterniflora*, with consequent building up of the peat level. The other side, to the contrary, appears to be enlarging, with abrupt vertical sides analogous to cliff recession.

ISLANDS

High spots in the marsh occur with great frequency in the Wequetequock-Pawcatuck area. Some of these are so large and so high that they bear tall forest and need not be differentiated from the "general upland" elsewhere mentioned. In other instances, for example the Till Islands, mineral glacial till comes close to the surface, causing a slight doming in the marsh, noted by its different vegetation. In still other instances, large glacial rocks rise out of the marsh, the Boulder Islands, bearing distinctive vegetation at their bases. Stranded Peat Blocks form the third type of vegetational island.

TILL ISLANDS

Till Islands are small areas where the soil surface is higher than the immediate surroundings, and where the vegetation differs. The Island vegetation may consist of one or more communities and, together with that of the surroundings, always represents some compressed segment of the normal Upland-to-Bay Sequence already described.

For example, a round patch of Juncus within an area of *Spartina patens* is frequently at a higher level. In a few instances, there may be no present observable difference in soil level. In turn, a patens island may be surrounded by the Forb Panne. In other cases, a fragment of the Panicum Border will be at a distinctly higher level, and perched on a mound of mineral soil which is overlain by several inches of peat. Such a Panicum Border may be ringed by Juncus, the combination occurring in an area of patens. If the center of the island is unusually high, a few weatherbeaten plants of Rhus, Myrica, and Vaccinium will represent the Shrub Border.

BOULDER ISLANDS

Boulder Islands are similar to Till Islands in many respects. They are extremely common in parts of the Area, appearing like boulders in an old field. That such rocks are not equally conspicuous in the adjoining upland leads one to surmise that the surrounding glacial till was removed at some past period by erosive action.

It is characteristic of the Boulder Islands that the flat marsh land is not always juxtaposed directly to the side of the boulder, but often rises through a horizontal distance of 30-60 cm. and a vertical distance of 2-15 cm. Such a slope is composed of peat, not of mineral soil, and would thus appear to be strictly a marsh phenomenon.

The annular vegetation belts of these islands resemble those of the Till Islands, and represent a compact segment of the Upland-Bay Sequence. In some cases, shrubs may be established on the boulder itself or at its base, while Upper Border, Upper Slope or Lower Slope communities will occur, depending upon the extent of the slope and the nature of the surrounding marsh.

STRANDED PEAT BLOCKS

In certain parts of the marsh near the bay, large blocks of peat are stranded irregularly. There are probably about fifty such blocks, varying from 0.5 to 2.0 m. in diameter, in addition to various smaller ones. These blocks have presumably been broken off from the eroding bay front, and washed up on the marsh during high tides.

The vegetation of these peat blocks is notable for the absence of any striking vegetational changes. The plants appear to continue growth with relatively little modification of form or density. This lack of change is despite the improved drainage, aeration, and leaching of salts which undoubtedly takes place. Occasionally Atriplex or Suaeda will become established on a bare side. The absence of invasion by other species may however be related to nothing more than the absence of propagules at such sites.

There is frequent evidence of scouring and degradation of the marsh level around the edges of the block. Such action is probably related to the erosive effects of tidal waters, as their velocity is increased in rounding these points.

ESTUARY EFFECTS

Tidal-marsh not only stretches from the upland out into the bay, but also extends up the narrow valleys, in finger-like projections. The streams themselves wind down over the tidal-marsh, and, being under tidal influences, are referred to as estuaries. These estuaries, and associated physiographic processes, give rise to certain distinctive vegetational sites. Three such sites markedly complicate the tidal-marsh mosaic, and deserve special consideration (Fig. 15).

ESTUARY BEDS

The bed of the estuary may be on peat or on glacial till, with or without protruding boulders. The plant life of the bed is sparse, and irregularly distributed. Zostera marina is frequently found at the estuary mouth, and occurs sparingly upstream. Ruppia maritima is fairly common. Zannichellia is relatively rare. Scirpus nanus was found on exposed mud at one station.

SPARTINA ALTERNIFLORA MARGINS

The margins of the estuaries are in constant flux. Some are being eroded by current action. Others are being built up by deposition or by peat-forming *Spartina alterniflora*. The Spartina alterniflora Lower Border, already described, extends up the margins of the estuaries with no observable change in its composition or structure.

JUNCUS NATURAL LEVEES

The most distinctive feature of the estuary sequence is the natural levee. At times of high water, the estuary overflows its banks. The velocity of this water is checked because of its shallowness and because of its flow through the dense grass. The load of silt and peat particles is soon dropped. Gradually this deposit builds up to form a low mound or natural levee. Such a levee affords a significantly different plant site.

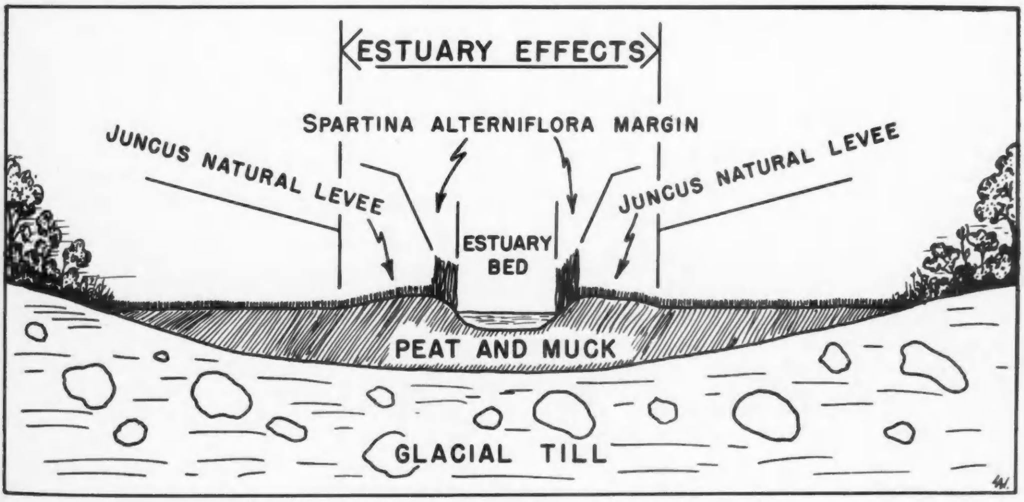


FIG. 15. Diagrammatic cross-section of the estuary effects.

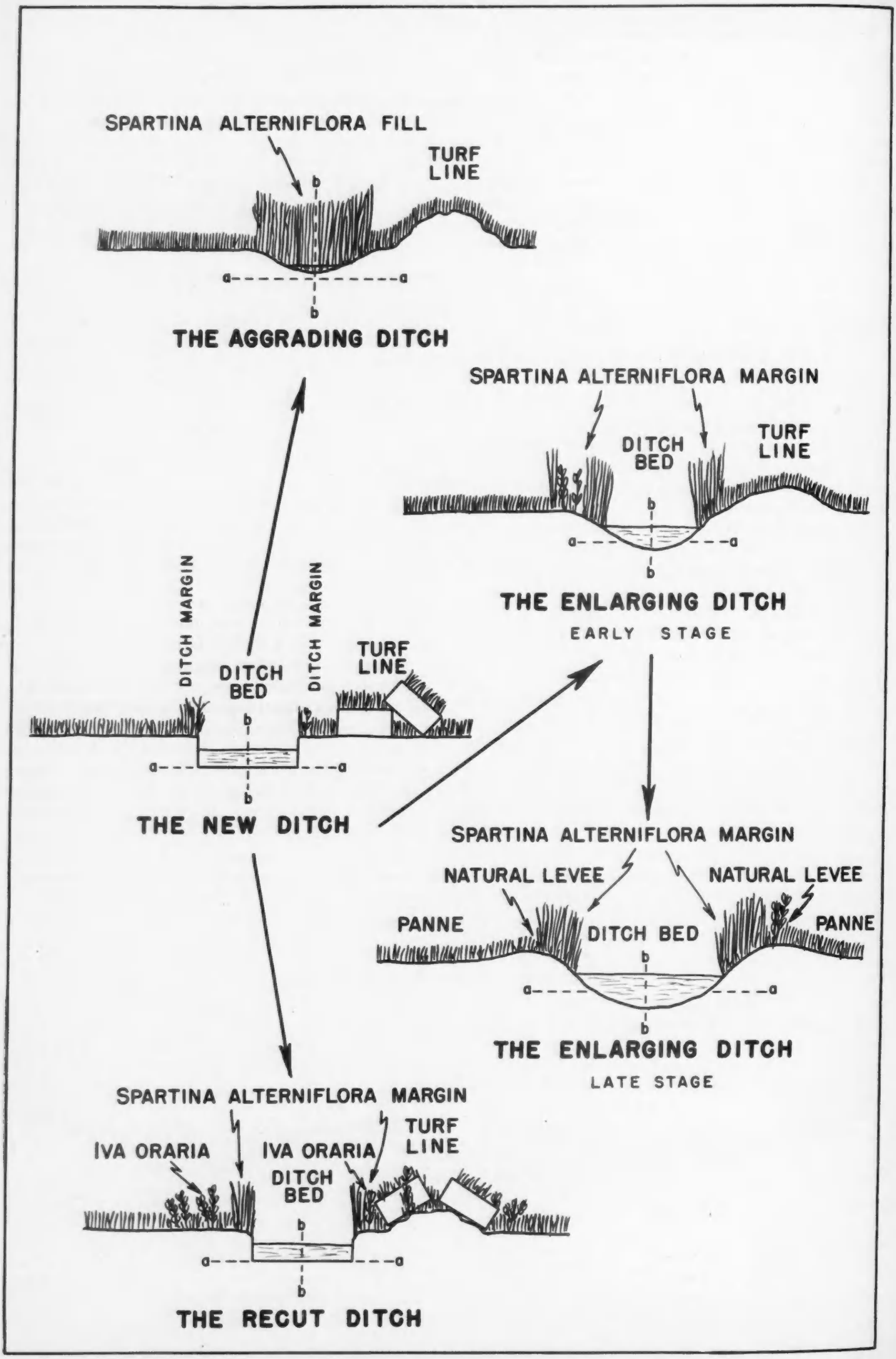


FIG. 16. Diagrammatic cross-section of the mosquito-ditch effects, not drawn to scale. A—A and B—B are the original horizontal bottom and vertical midlines of the ditch.

These levees in the area are estimated to be commonly 30-45 cm. in height and 5-10 m. broad. The existence of such a levee was very forcibly shown in 1947 during the unexpected drying of Impoundment 1. At a certain level of water, the levees emerged as two narrow arcuate islands bordering each side of the estuary channel.

The vegetation of the natural levee is a Juncus community, not observably different from that of the Juncus Upper Slope already described. It is reasonable to suppose that the ecologic conditions of these two sites, Upper Slope and Natural Levee, are essentially similar for the development of vegetation.

MOSQUITO-DITCH EFFECTS

The omnipresent mosquito-ditch had an initial and immediate effect in changing the entire aspect of the original marshes when they were constructed in 1931-32, that is, by draining the Ruppia Pools. In addition, it is causing far more fundamental and deep-seated changes by affecting deposition and erosion, and thus regulating level changes in every square foot of the marsh. Even when eventually obliterated by filling-in of peat, different plants will long persist in the line of the ditch.

From the standpoint of vegetation, the ditches exist in infinite variety. No two are exactly the same, and the condition of any one ditch may change completely within the length of several feet. A classification of ditches, therefore, must necessarily be highly artificial, and can only provide points of orientation by which to describe various concrete examples. For present purposes, four types will be considered: new ditches, aggrading ditches which are filling in, enlarging ditches, and re-cut ditches (Fig. 16).

NEW DITCHES

A newly dug ditch is a mechanically excavated channel about 30 cm. wide and 50 cm. deep. The excavated sod is thrown in a line paralleling the ditch, and forms a mound hereafter referred to as the Turf Line. Almost immediately, certain new sites for plant life are created, of which three are mentioned in the paragraphs following.

The Ditch Bed. Some ditch beds may be deep enough to be almost permanently submerged. If so, Ruppia occasionally establishes itself, and the site becomes effectually a peninsula-like extension of the estuary beds. In other instances, seed-plants are absent.

The Ditch Margin. The vertical sides of the mosquito ditch hold their form and remain in place for a remarkably large number of years, considering that the substratum is only peat. The bare sides however are eventually invaded by plants, chief of which is *Spartina alterniflora.* Various forbs are apt to occur, often growing taller and more luxuriantly than in the immediate vicinity. Locally Suaeda is common on these edges. This species, though typical of the tidal-marshes, was conspicuous by its absence in the various plot studies already described. The shrubby Iva often appears. Its role will be discussed later.

The Turf Line. This line, in these early stages, is not distinguished by an invading or conspicuous species. The plants already in the turf continue to develop with little change.

AGGRADING DITCHES

In those cases where vegetational development gains the ascendency over eroding effects of flowing water, aggradation takes place. The marginal alterniflora extends into the ditch and serves even further to cut off the flow of water. A turf of fibrous root stocks is built up, and the level tends to approach that of the general marsh. In favorable instances a line of alterniflora fill may occupy a shallow depression continuously for distances of 30-50 meters.

The development of the Turf Line presents some anomalous and as yet unexplainable variations. In general, the turf blocks settle, and tend to become a hummocky line. The vegetation may be no different from that of the general marsh. At other times, it may bear forbs of good growth. At one site, the Line is predominantly of *Spartina patens* in a Juncus marsh. In other cases, *Spartina patens,* Distichlis, and Juncus occur in significantly different proportions.

ENLARGING DITCHES

Early Stage. In those cases where the ditch is subject to considerable tidal effects, with ample flow of water, control of the banks by vegetation is at a minimum. To the contrary, degradational and aggradational physiographic processes are paramount.

In general, a ditch tends to enlarge. Such enlargement is related to the erosive effects of currents, as assisted by the numerous burrows of the fiddler crabs. Furthermore, the ditch sides tend to slump. Along with these processes, the alterniflora margins tend to widen and to separate outwards. Iva may be present in variable quantity. The surface of the Turf Line becomes smoother, in part due to the flow of the high tides over its surface.

Late Stage. In ditches subject to considerable tidal movements, the conditions begin to approximate those of a small estuary. Scour and erosion tend to enlarge the channel, which in some cases may become half again as wide as the original ditch. The *Spartina alterniflora* margins spread apart, accordingly. Iva is present in variable quantity. Perhaps the chief development of this Late Stage is the deposition of small, but highly important, natural levees. As in the case of the estuary above described, high tide waters flow out from the ditch. The velocity decreases because of decrease in depth and because of blocking by vegetation. The load of silt and organic particles is dropped. Factual evidence for natural levee development along ditches was observed some 32 km. to the east in a lagoon marsh on sand. At this locality, ditches had been cut in the grassy marsh, bisecting various low bare sandy spots. At such spots, natural levees 5-10 cm. above the general level of the bare sand lined both sides of the ditch.

RE-CUT DITCHES

The majority of the ditches do not have enough tidal flow to keep them open, and they are recut at intervals. In such cases, the turf removed is piled over the old Turf Line.

Such ditches do not have any sizable alterniflora margin, since that which is formed in the ditch is removed by recutting. Neither do they have any well-developed natural levee, because of the minor quantity of silt-laden tidal waters. In other respects, they resemble the ditches already discussed. Their chief physiognomic characteristic, in about one quarter of the cases, is the presence of the shrub Iva, in belts about one meter wide on each side of the ditch.

THE IVA COMMUNITY OF ALL DITCHES

Iva oraria is almost entirely absent from large stretches of the open marsh. It is present in varying degrees, with Coverage from 0-95 percent, along the edges of the various types of ditches. Rarely, it will reach a Coverage of 50 percent in the otherwise normal marsh between ditches. In height, the plant is commonly 0.5-1.0 meters. In shape and color of foliage, and woodiness, the plant is extremely conspicuous when on the marsh. Herbaceous vegetation growing with it is thin and depauperate, otherwise there is little change in community structure and composition.

The "Iva problem" has received considerable attention in the literature, albeit it is a "problem" only to those who do not see in it a wholly natural though unexpected trend in vegetation development. In much of New England and New York, Iva borders the mosquito ditches regularly, for acres at a time. Previous researchers have drawn the conclusion that since it has not spread any farther than it has in 20 years, the matter cannot become a problem. (One might, with parallel logic and the same data, argue that if the plant effects the same advance every 20 years, the matter *is* a problem.)

Observations in connection with the present study do not permit any definite conclusions as to the community role of Iva. It is true that large areas of marsh are yet uninvaded, even along the ditches. It is also true that in some areas Iva has not only filled the ditch banks but has fairly well covered the marsh between the ditches, as seaward of Dike 1, west side. Close observation of a large number of individual plants indicates no evidence of a general retrogression or dying out of individuals in the current years. To the contrary, that there are plants of various sizes near the older individuals indicates an areal advance of the colony. Furthermore, the number and size of shoots per plant one season were always greater than those of the previous season. Furthermore, innumerable seedlings in the Juncus and patens types show a land area potentially able to go to Iva when and if the rush and grass ever produce a thinner cover. In short, the Iva gives all evidence, at this time, of effecting a very slow but cumulative increase in area.

The question arises as to why this colonization by Iva should have started with the recent ditching, and should not have been brought to completion several millenia ago. Although the ditches form the present spearheads for invasion, the fact that Iva has more or less completely invaded sites not under the direct control of ditches (and also that Iva was not so spread in colonial times) means indubitably that other factors are involved. Until the role of fire and mowing on the marshes is studied by modern research methods, these factors must be under suspicion. How many additional factors are concerned, it is impossible to ascertain with the knowledge now available.

DEVELOPMENT OF NEW PANNES

The ditch-side levees, mentioned above in the discussion of the enlarging ditch, have a very important and significant effect. These levees, ipso facto, tend to convert the entire inter-ditch marsh into a panne. Such a panne then tends to hold the water and to produce the very kind of pool which the ditch was originally designed to drain. These new pannes are rectangular in shape, and alternate regularly with the ditches and their levees. The phenomenon is noticeable on the west side of impoundment 1 (Fig. 17), despite the flooding of this area. It is also apparent after high tides in the front marshes before headquarters. To what extent this phenomenon may progress and become of significance in mosquito control, as well as to the vegetation, is still uncertain.

FIG. 17. New pannes, as developed by the levee effect along mosquito ditches, under conditions of impoundment. Large inter-ditch panne in central foreground. West side of Impoundment 1, looking east from Photo-station 30.

MOWING EFFECTS

Various phenomena of (a) community disintegration, (b) sheet erosion, and (c) revegetation of the Upland Border and the Upper Slope are here interpreted in terms of excessive mowing (Fig. 18). It is to be understood that this explanation is strictly an interpretation, believed in accord with our contemporary knowledge in the fields of range and pasture management and soil conservation. No experimentation has been carried on, though it is much to be desired.

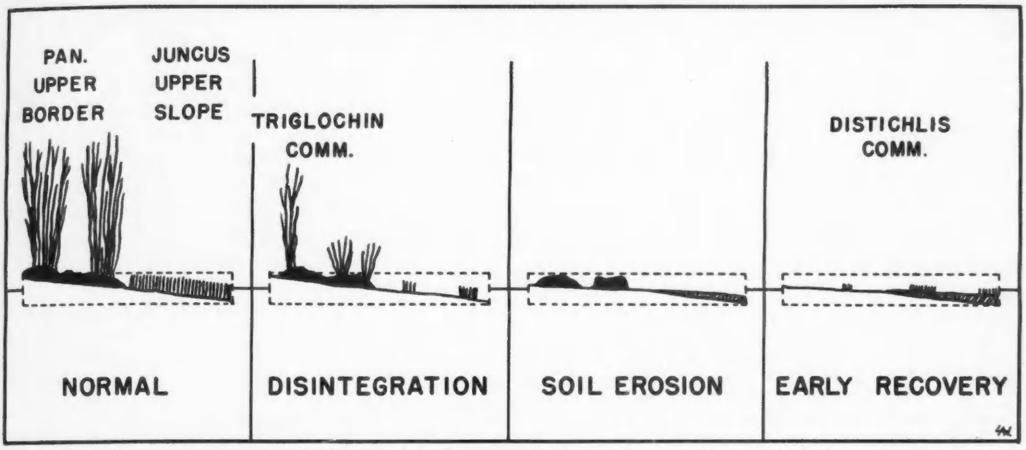


FIG. 18. Diagrammatic representation of the effects of mowing on the vegetation of the Upper Border and the Upper Slope, as interpreted from historical and contemporary conditions.

The mowing history of the area is known only incompletely. The Davis Marsh is believed to have been mowed continuously since colonial days. Other parts of the marsh are known to have been mowed frequently up to 10 or 20 years ago, for hay used for bedding and packing. At the present time, one part of the Brucker Marsh is mowed, and it is here that the effects are most conspicuous.

DISINTEGRATION: THE MOWED FORB COMMUNITY

Along the seaward borders of the Brucker Marsh, the vegetation is thin, scanty, or absent in a belt easily correlated with the normally dense Panicum Upper Border and the Juncus Upper Slope. Elsewhere in this marsh, parts of these two belts are bare and barren. Observation quickly discloses the dead or decadent bases of plants normally growing in tussocks, especially *Panicum virgatum,* also Triglochin and Plantago. Sometimes the tussock is completely dead; sometimes only one or two green shoots survive.

At least two factors are theoretically involved in the disintegration of this community by mowing. The Panicum Border is a tussock grassland, with 75 percent of the space covered primarily by a natural mulch of dead grass. In the first place, repeated mowing destroys the normal increment to this mulch. Eventually with decay and disappearance of the old mulch, the soil is left bare. Dyksterhuis and Schmutz (1947) have recently considered the importance of such a natural mulch on a Texas prairie. Secondly, repeated cutting is assumed to affect the growth and vigor of the plants. For example, Weaver and Darland (1947) have recently reported on the decreased vigor of various grasses from a Nebraska prairie grown and clipped experimentally. *Panicum virgatum* itself was used, and showed considerably reduced root systems under such clipping.

As the *Panicum virgatum* is gradually destroyed by repeated mowing, certain forbs emerge into dominance, chief of which appear to be Triglochin and Plantago. These and other forbs may become so abundant that a Mowed Forb or Triglochin Community comes into existence. Actually, no extensive stretch of this community was found for study, but sufficient relicts were located to establish its identity. The relicts were dead root-mounds, interpreted as destruction caused by continuous and excessive mowing. The fact that Triglochin becomes abundant may be of considerable practical importance, as this plant is a species known to be poisonous to cattle and other stock.

SHEET EROSION

With continued mowing, the higher belts eventually become bare. Although the marsh is essentially a flat area, both Upper Border and Upper Slope have

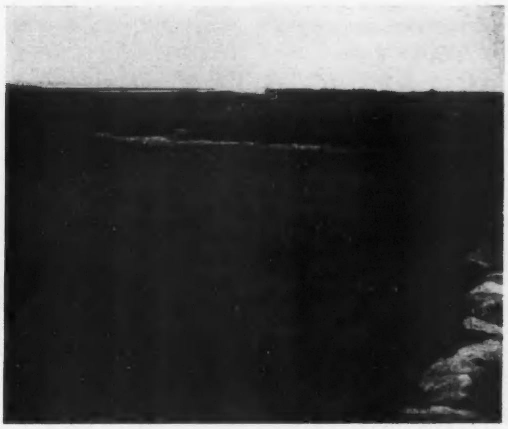


FIG. 19. Erosion on the margins of a *Panicum virgatum* and *Juncus gerardi* "island" in the tidal-marsh (center and right center). The black border is the undercut and receding margin of the eroding soil. The light strip, about one meter wide, is the eroding zone, in part invaded by Distichlis. Seaward of Headquarters Island, looking south from Photo-station 14.

enough gradient so that in the absence of vegetative cover the soil is subject to surface erosion. The customary attendant phenomena were noticed: erosion around the dead bases of the tussock plants, leaving the mounds 5-10 cm. above the new level; degrading swaths several meters or so wide with undercut margins; aggrading areas a meter or so wide below the swaths (Fig. 19).

RECOVERY WITH DISTICHLIS

In certain localities, notably in the marsh before headquarters, Distichlis is obviously and successfully in process of invading the new sites bared by sheet erosion. The plant covers certain spots sparsely though continuously. At the edge of such a colony, the plant may be actively invading farther as indicated by the manner in which young rhizomes of healthy growth extend outwards.

The developmental stages following this pioneer community have not been observed.

THE ULTIMATE VEGETATION

There exist today only certain indications of the tidal-marsh vegetation of the future. Logically, one may segregate the geomorphic development from the purely vegetational development.

Geomorphic development points toward a gradual rising of the level of the marsh, and a bodily landward shift of the entire marsh. In this respect, the botanic marsh rides along essentially unchanged, each belt replacing the belt on its landward side. From the point of view of ultimate shoreline development, however, headlands will be removed, bays aggraded, the coast will be characterized by a straight sandy beach. In this respect, our tidal-marsh is entirely destroyed, and with it, our botanic problem.

Vegetational development is a phenomenon usually occurring on a much shorter time-scale. Studies on the Wequetequock-Pawcatuck marshes and elsewhere do not, in the opinions of the authors, afford sufficient data to hypothesize the "ultimate vegetation." By ultimate vegetation is meant that which would develop in the absence of those factors called "abnormal," such as fire, mowing, and ditching. Long-term basic research is needed before a suitable hypothesis can be developed. It is reasonably certain that the Upper Border, Upper Slope, Lower Slope and Lower Border will remain, together with the modifications induced by natural levees, islands, and compaction spots. The role of Iva is probably the greatest single unknown factor. There is some evidence that this is a slow but cumulative invader, previously eliminated by Indian fires and colonial mowing. The ultimate degree of such invasion, and with it the problem of grassland versus scrub, cannot as yet be foretold.

SUMMARY

The Wequetequock-Pawcatuck saline tidal-marshes are a single compact area in extreme southeastern Connecticut, owned mainly by the Connecticut State Board of Fisheries and Game, and administered for research and development as a public shooting area.

The vegetation is a complex mosaic of many communities, correlated with tidal effects, average salinities, extreme salinities, surface levels, soil acidity and peat development, compaction and disintegration. Figures and diagrams show the composition and structure of these communities, and their topographic and edaphic relations to each other. The vegetation of the impounded area is not here reported upon.

A simplified upland-to-bay sequence involves four vegetational belts: a Panicum virgatum Upper Border, dominated by that species and *Spartina pectinata;* a Juncus gerardi Upper Slope, a Spartina patens Lower Slope; and a Spartina alterniflora Lower Border.

Depressions are of two kinds: shallow pannes, and deep potholes. Pannes, closely correlated with evaporation and lethal concentrations of salts, show some combination of the following: more or less permanent Ruppia pools; bare salt pannes; a stunted Spartina alterniflora community; and forb pannes of many herbs. Potholes, of unknown genesis, appear to be enlarging in some cases and contracting in others.

Islands in the marsh, being boulders or masses of glacial till, possess various concentrically arranged communities typical of higher levels. Stranded peat blocks, seldom more than a meter in diameter, possess no distinctive vegetation.

Estuaries are lined by *Spartina alterniflora* communities. Broad low natural levees frequently develop, covered with the Juncus community of the Upper Slope.

Mosquito ditches not only produce distinctive sites at their margins, but because of drainage of the pools and the development of natural levees at their sides, they have far-reaching effects on the entire mosaic of the tidal-marsh, at times producing new pools between parallel ditches.

Mowing appears to produce a disintegration of the Upper Border and the Upper Slope. Eventually the soil is bared, and sheet erosion occurs.

The ultimate vegetation of the tidal-marsh in the absence of fire, mowing and ditching cannot be foretold with certainty. The future role of the shrubby Iva is the most important single unknown factor. Evidence today implies a slow cumulative increase in this species.

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